General Physiology, Experimental Psychology, and Evolutionism

Unicellular Organisms as Objects of Psychophysiological Research, 1877–1918

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ABSTRACT

This essay aims to shed new light on the relations between physiology and psychology in the late nineteenth and early twentieth centuries by focusing on the use of unicellular organisms as research objects during that period. Within the frameworks of evolutionism and monism advocated by Ernst Haeckel, protozoa were perceived as objects situated at the borders between organism and cell and individual and society. Scholars such as Max Verworn, Alfred Binet, and Herbert Spencer Jennings were provoked by these organisms to undertake experimental investigations situated between general physiology and psychology that differed from the physiological psychology advocated by Wilhelm Wundt. Some of these investigations sought to locate psychological properties in the molecular structure of protoplasm; others stressed the existence of organic and psychological individuality in protozoa. In the following decades, leading philosophers such as Friedrich Nietzsche, Charles Sanders Peirce, and Henri Bergson, as well as psychological researchers like Sigmund Freud, integrated the results of these investigations into their reflections on such problems as the nature of the will, the structure of the ego, and the holistic nature of the reactions of organisms to their environment.

IN 1929 THE HARVARD PSYCHOLOGIST EDWIN G. BORING introduced a grand narrative of the development of experimental psychology that continues to inform much contemporary history of psychology. In his widely cited *History of Experimental Psy-*

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chology, Boring traced the intellectual ancestry of the well-known pioneer of experimental psychology Wilhelm Wundt to the idealist philosopher Immanuel Kant and the experimental physiologist Hermann von Helmholtz. By emphasizing Wundt's ties to Helmholtz, Boring perpetuated the views of Wundt's contemporaries, who attributed the success of his 1874 *Grundzüge der physiologischen Psychologie* [*Principles of Physiological Psychology*] to his rigorous engagement with the exact sciences during a six-year tenure in Helmholtz's laboratory. According to this interpretation, experimental psychology was the synthetic outcome of Helmholtzian experimental physiology and idealist philosophy and Wundt was the first scholar in postidealist Germany "who without reservation is properly called a psychologist."[1]

Despite the revised and enriched understanding of Wundt's intellectual and professional development that has emerged in recent years, there has been insufficient historical reevaluation of the emergence and development of physiological psychology itself.[2] Robert Richards has contributed to our understanding of the development of modern psychological thought by demonstrating the importance of evolutionary theory in shaping the scholarship of some of the same scientists who played significant roles in Boring's account, including C. Lloyd Morgan, George Romanes, William James, and James Mark Baldwin.[3] Yet Richards only hints at connections between the theories of these evolutionary thinkers and the development of experimental research at the intersection of physiology and psychology, as depicted by Boring. In this essay we aim to bridge the gap between these accounts.

[1] Edwin G. Boring, *A History of Experimental Psychology* (New York: Appleton-Century, 1929), p. 310. Boring studied at Cornell with Edward Titchener, who studied with Wundt in Leipzig in the early 1890s. On Boring see John M. O'Donnell, "The Crisis of Experimentalism in the 1920s," *American Psychologist,* 1979, *34:*289–295; and James H. Capshew, *Psychologists on the March: Science, Practice, and Professional Identity in America, 1929–1969* (Cambridge: Cambridge Univ. Press, 1999). For the views of Wundt's contemporaries see, e.g., William James, "Review of *Grundzüge der physiologischen Psychologie* by Wilhelm Wundt," in *The Works of William James,* ed. Frederick J. Burkhardt, 19 vols. (Cambridge, Mass.: Harvard Univ. Press, 1975–1988), Vol. 7, pp. 296–303; and Désiré Nolen, "Introduction," in Wilhelm Wundt, *Éléments de psychologie physiologique,* trans. Élie Rouvier (Paris: Alcan, 1886), pp. vii–xxv.

[2] See, e.g., Robert W. Rieber and David K. Robinson, eds., *Wilhelm Wundt in History: The Making of a Scientific Psychology* (New York: Kluwer, 2001); Robinson, "Wilhelm Wundt and the Establishment of Experimental Psychology: The Context of a New Field of Scientific Research" (Ph.D. diss., Univ. California, Berkeley, 1987); and Kurt Danziger, *Constructing the Subject: Historical Origins of Psychological Research* (Cambridge/New York: Cambridge Univ. Press, 1990). See also Arthur L. Blumenthal, "A Reappraisal of Wilhelm Wundt," *Amer. Psychol.,* 1975, *30:*1081–1088, on Wundt's impact on linguistics; Gary Hatfield, "Wundt and Psychology as Science: Disciplinary Transformations," *Perspectives on Science: Historical, Philosophical, Social,* 1997, *5:*349–382, on institutional aspects of Wundtian psychology; and Ruth Benschop and Douwe Draaisma, "In Pursuit of Precision: The Calibration of Minds and Machines in Late Nineteenth-Century Psychology," *Annals of Science,* 2000, *57:*1–25, on the Leipzig laboratory culture. Among those works to perpetuate Boring's narrative is the classic essay by Joseph Ben-David and Randall Collins, "Social Factors in the Origins of a New Science: The Case of Psychology," *American Sociological Review,* 1966, *31:*451–465; Raymond E. Fancher, *Pioneers of Psychology* (New York/London: Norton, 1979); David Hothershall, *History of Psychology* (New York: Random House, 1984); and Leslie S. Hearnshaw, *The Shaping of Modern Psychology* (London/New York: Routledge & Kegan Paul, 1987).

[3] Robert J. Richards, *Darwin and the Emergence of Evolutionary Theories of Mind and Behavior* (Chicago: Univ. Chicago Press, 1987). As Richards points out, Wundt provided a theoretical framework informed by evolutionism in his 1863 *Vorlesungen über die Menschen- und Thierseele,* 2 vols. (Leipzig: Voss), which allowed him to consider infusoria as conscious beings situated at the base of the ladder of psychological life: Richards, *Darwin and the Emergence of Evolutionary Theories of Mind and Behavior,* pp. 521–522. These earlier evolutionist views did not play a significant role, however, when Wundt started his laboratory work in physiological psychology at Leipzig in 1879. By the time of the publication of the second edition of the *Vorlesungen,* in 1893, Wundt had abandoned the inclusion of infusoria and other animals in his psychological theory. On Wundt's shifting evaluation of Darwinian theory see Richards, "Wundt's Early Theories of Unconscious Inference and Cognitive Evolution in Their Relation to Darwinian Biopsychology," in *Wundt Studies: A Centennial Collection,* ed. Wolfgang G. Bringmann and Ryan D. Tweney (Toronto: Hogfrefe, 1980), pp. 42–70.

We offer new evidence that the relations between physiology and psychology in the late nineteenth and early twentieth centuries were much more complex than the well-known case of Wundt suggests.[4] Rather than focusing on one dominant "physiological psychology" associated with Helmholtz and Wundt, we examine another group of scientists who also shared fundamental assumptions about the close connections between physiology and experimental psychology. The German general physiologist Max Verworn (1863–1921), the French scholar Alfred Binet (1857–1911), who today is known primarily as a pioneer of child psychology and mental testing, and the American zoologist Herbert Spencer Jennings (1868–1947) each engaged in experimental "psychophysiological" studies that, we argue, paralleled Wundt's own endeavor in physiological psychology. The investigations of these three differed significantly from the activities in Wundt's Leipzig laboratory, however, since they were built on the foundations of evolutionism, *Entwicklungslehre,* and monism.

Our argument assumes that, in addition to experimental physiology, or "organic physics," in the sense espoused by Helmholtz, Carl Ludwig, and Emil Du Bois-Reymond, there was another important physiological tradition that had a significant impact on experimental psychological research at the end of the nineteenth century. Following the establishment of cell theory and the advent of Darwinism in the middle decades of the century, eminent scholars such as Claude Bernard championed a field of "general physiology" that sought to discern the properties of life common to all living beings.[5] In contrast to those who adhered to the "organic physics" tradition of physiology, researchers striving to establish a general physiology did not concentrate their experimental practices on higher organisms such as frogs, rabbits, or dogs. Instead they focused on the cell, or "elementary organism," as their primary object of study, since it was deemed to be both the only functional organic entity common to both plants and animals and the natural starting point of physiological as well as psychological life. When it was established in the 1870s that microorganisms such as paramecia and amoebas were unicellular beings, scholars began to employ them as models of cells. As they delineated cells and unicellular organisms—the latter referred

[4] For other literature that aims to complicate the dominant narrative see Lorraine Daston, "British Responses to Psycho-Physiology, 1860–1900," *Isis,* 1978, *69:*192–208; Kurt Danziger, "Mid-Nineteenth-Century British Psycho-Physiology: A Neglected Chapter in the History of Psychology," in *The Problematic Science: Psychology in Nineteenth-Century Thought,* ed. William Woodward and Mitchell G. Ash (New York: Praeger, 1982), pp. 119–146; and Roger Smith, *Inhibition: History and Meaning in the Sciences of Mind and Brain* (Berkeley: Univ. California Press, 1992). See also the early study by Franklin Fearing, *Reflex Action: A Study in the History of Physiological Psychology* (Baltimore: Williams & Wilkins, 1930).

[5] On "organic physics" see Paul F. Cranefield, "The Organic Physics of 1847 and the Bio-physics of Today," *Journal of the History of Medicine and Allied Sciences,* 1957, *12:*407–423; Timothy Lenoir, "Social Interests and the Organic Physics of 1847," in *Science in Reflection: The Israel Colloquium: Studies in History, Philosophy, and Sociology of Science,* ed. Edna Ullmann-Margalit (Dordrecht/Boston/London: Kluwer, 1988), pp. 169–191; and Joseph Ben-David, "Social Interests and the Organic Physics of 1847: A Comment," *ibid.,* pp. 193–200. On Bernard's view of general physiology see, e.g., Claude Bernard, *Rapport sur les progrès et la marche de la physiologie générale en France* (Paris: Imprimerie Impériale, 1867). On cell theory see Marc Klein, "Histoire des origines de la théorie cellulaire," in *Regards d'un biologiste* (1936; Paris: Hermann, 1980), pp. 7–69; Everett Mendelsohn, "Cell Theory and the Development of General Physiology," *Archives Internationales d'Histoire des Sciences,* 1963, *16:*419–429; François Duchesneau, *Genèse de la théorie cellulaire* (Montreal: Bellarmin, 1987); and Ohad Parnes, "The Envisioning of Cells," *Science in Context,* 2000, *13:*71–92. On general physiology in the nineteenth century see Thomas S. Hall, *Ideas of Life and Matter: Studies in the History of General Physiology, 600 B.C. to 1900 A.D.,* 2 vols. (Chicago: Univ. Chicago Press, 1969), esp. Vol. 2, pp. 121–382; John V. Pickstone, "The Origins of General Physiology in France, with Special Reference to the Work of R. J. H. Dutrochet" (Ph.D. diss., Chelsea College, Univ. London, 1973); and Leon S. Jacyna, "Principles of General Physiology: The Comparative Dimension to British Neuroscience in the 1830s and 1840s," *Studies in the History of Biology,* 1984, *8:*47–93.

to as "protists," "protozoa," or "infusoria"—as the research objects of general physiology, investigators began to consider the relevance of these organisms for related domains of scientific inquiry.[6]

It was just a short time later that protozoa began to appear in articles and monographs dedicated to experimental psychology. Unicellular organisms made their debut in this context in 1887, when Binet published his study on "the psychic life of micro-organisms." Two years later Verworn presented the results of his psychophysiological experiments with protozoa, before going on to publish one of the classic textbooks on general physiology. In 1906 Jennings published his well-known text detailing extensive experiments on the behavior of lower organisms, before turning to the exciting new field of genetics. Each of these studies not only explored general physiological questions about the basic properties of all living beings but, as we will show, addressed important psychological questions about the evolution of individuality, consciousness, and agency in the living world.[7]

In addition, experimental studies of protozoa captivated turn-of-the-century philosophers, who found that these investigations illuminated a broad range of fundamental problems at the intersection of philosophy and the life sciences. Friedrich Nietzsche (1844–1900) and Charles Sanders Peirce (1839–1914), for example, drew on psychophysiological research on protozoa and protoplasm when considering the physiological and chemical basis of complex psychological functions such as thought, feeling, and judgment. For other philosophers, such as Henri Bergson (1859–1941) and Max Scheler (1874–1928), protozoa were important examples for illustrating the relationship between organic and psychological individuality. More broadly, philosophers referred to psychophysiological studies of protozoa to argue against a mechanistic science of life that strove to reduce the basic properties of living beings to reflex phenomena or chemical processes. And, around 1915, Sigmund Freud (1856–1939) adopted protozoa as general models for the "psychological apparatus" and particularly of its "ego" functions in psychoanalysis.

Our investigation of this sphere of psychophysiological research and thought in the late nineteenth and early twentieth centuries focuses not on career patterns and institutional developments but on closely related scientific objects—cells and protozoa. By tracing the movements of these objects into different domains of experimental and nonexperimental

[6] On the choice of the cell as the focus of study see, e.g., Max Verworn, *General Physiology: An Outline of the Science of Life,* trans. F. S. Lee from the 2nd German ed. (London: Macmillan, 1899), p. 50. The popular term "infusoria," or "infusion animals," stemmed from the common wisdom that these organisms were found in grass or hay infusions; by the nineteenth century, the term referred to a subgroup of the protozoa known today as the "ciliates." The term "protozoa," or the German word "*Urthiere,*" designated, according to its Greek etymology, "primitive" or "first animals." In his *Generelle Morphologie der Organismen* (Berlin: Reimer, 1866), Ernst Haeckel introduced the evolutionary-based concept of "protists," meaning "the ones who came first in time." Haeckel's term is used today to refer to approximately two hundred thousand species of mostly unicellular eukaryotic algae, "lower" fungi, and protozoa. See Lynn J. Rothschild, "Protozoa, Protista, Protoctista: What's in a Name?" *Journal of the History of Biology,* 1989, *22:*277–305. On subsequent developments in general physiology in the twentieth century see Robert E. Kohler, *From Medical Chemistry to Biochemistry: The Making of a Biomedical Discipline* (Cambridge: Cambridge Univ. Press, 1982), pp. 286–323, esp. pp. 307–313; and Philip J. Pauly, "General Physiology and the Discipline of Physiology, 1890–1935," in *Physiology in the American Context, 1850–1940,* ed. Gerald E. Geison (Bethesda, Md.: American Physiological Assoc., 1987), pp. 195–207.

[7] Alfred Binet, "La vie psychique des micro-organismes," *Revue Philosophique de la France et de l'Étranger,* 1887, *24:*449–489, 582–611; Max Verworn, *Psycho-physiologische Protistenstudien: Experimentelle Untersuchungen* (Jena: Fischer, 1889); and Herbert S. Jennings, *Behavior of the Lower Organisms* (1906; Bloomington, Ind.: Indiana Univ. Press, 1976). These studies were also consonant with the nascent field of "general psychology" as it was envisioned in 1887 by the future Nobel laureate in physiology, Charles Richet. See Charles Richet, *Essai de psychologie générale* (Paris: Alcan, 1887).

research, we are able to elucidate relationships between physiology, psychology, and philosophy not previously ascertained by other historical methods. Although our approach shares a common inspiration with recent investigations of the history of research objects in the life sciences, we focus less on the material instrumentality of objects emphasized by these studies and more on their role as entities stimulating scientific activity of various kinds. We are concerned with how specific research objects that were situated at the borders of recognized domains in the natural world provoked experimental activities, ideas, and assumptions and with how these activities, ideas, and assumptions were transported along with the objects into other scientific and nonscientific domains.[8]

We argue that, as "provocative objects," protozoa stimulated not only the thoughts of turn-of-the-century scholars but also the actual conduct of research programs and the transport of associated ideas and practices to new domains.[9] Protozoa provoked fundamental scientific questions about the nature of the organic individual, the relation between the physiological and the psychological, and the origins of consciousness.[10] In their studies of unicellular organisms in the late nineteenth century, scholars hoped to answer such questions as, Are the adaptive movements of protozoa an expression of will and consciousness or simply the result of chemical processes? Do protozoa have sensations and perceptions, even if they do not have a nervous system and sense organs? Are protozoa individuals? If so, what is the source of their individuality? And if they are individuals, do they organize in larger entities that can be called social? When contemplating such questions, these investigators maintained that protozoa were elementary or primitive organisms that, according to the lessons of cell theory and Darwinism, should be the objects of *physiological* research. Yet they also recognized that these organisms manifested fundamental *psychological* properties found in humans—such as irritability, sensibility, and learning—albeit in a less complex form. Moreover, the close association of these psychological concepts with protozoa and their transport to other domains provoked both the use of political metaphors in the scientific study of protozoa, on the one hand, and the consideration of social and educational problems related to such investigations, on the other.

Long before they straddled the domains of the physiological and the psychological at the end of the nineteenth century, protozoa were viewed as curious objects situated at numerous other recognized borders of the living world. We begin with a brief examination

[8] See also Lorraine Daston, ed., *Biographies of Scientific Objects* (Chicago: Univ. Chicago Press, 2000). For studies that focus more on the material instrumentality of objects see, e.g., Adele Clarke and Joan H. Fujimura, eds., *The Right Tools for the Job: At Work in Twentieth-Century Life Sciences* (Princeton, N.J.: Princeton Univ. Press, 1992); Robert E. Kohler, *Lords of the Fly:* Drosophila *Genetics and the Experimental Life* (Chicago: Univ. Chicago Press, 1994); and Hans-Jörg Rheinberger, *Toward a History of Epistemic Things: Synthesizing Proteins in the Test Tube* (Stanford, Calif.: Stanford Univ. Press, 1997).

[9] In *The Second Self: Computers and the Human Spirit,* Sherry Turkle introduces the term "evocative object" to describe and analyze the reception of computer technology by the general public and, in particular, by the community of students and scholars active in the computer sciences. She uses the word "evocative" to describe how a technological object (in her case, the personal computer) "fascinates, disrupts equanimity, and precipitates thought": Sherry Turkle, *The Second Self: Computers and the Human Spirit* (New York: Simon & Schuster, 1984), p. 13. We have chosen the related but more dynamic term, "provocative object," for the reasons discussed in the text.

[10] On the problem of organic individuality see Lynn K. Nyhart, "The Problem of the Organic Individual in Mid-Nineteenth-Century Germany," paper presented at the University of Minnesota, Wangensteen Library, 15 May 1989; and Ruth Rinard, "The Problem of the Organic Individual: Ernst Haeckel and the Development of the Biogenetic Law," *J. Hist. Biol.,* 1981, *14:*249–275. On the impact of the conception of organic individuality on literature and philosophy in the nineteenth century see Andrea Orsucci, *Dalla biologia cellulare alle scienze dello spirito: Aspetti del dibattito sull'individualità nell'Ottocento tedesco* (Bologna: Società Editrice di Mulino, 1992); and Laura Otis, *Membranes: Metaphors of Invasion in Nineteenth-Century Literature, Science, and Politics* (Baltimore/London: Johns Hopkins Univ. Press, 1999), esp. pp. 8–36.

of the history of protozoa as provocative objects in the life sciences, culminating with the recognition in the 1870s that protozoa occupied the organizational juncture between cells and individual organisms. We then examine the bold program of psychological research on cells and protozoa sketched out in 1877 by the well-known zoologist Ernst Haeckel (1834–1919), which capitalized on the novel dual status of protozoa as unicellular organisms. On the basis of his belief that cells are individuals of the first order, Haeckel maintained that every cell—and therefore all protozoa—possessed a psyche that manifested the fundamental properties of psychological life.

Haeckel's vision was first realized in the psychophysiological studies of protozoa conducted by Verworn and Binet at the end of the 1880s and by Jennings about ten years later. We analyze the research programs of these three investigators, which built on many of the assumptions first outlined by Haeckel. We then trace the subsequent paths and impact of protozoa as provocative objects, both in the later careers of Verworn, Binet, and Jennings and in the psychological and philosophical queries of numerous other leading scholars at the beginning of the twentieth century. We find that the concepts explored in the experimental study of protozoa, such as individuality and psychophysiological adaptivity, continued to provoke productive study and contemplation in fields far removed from the protozoological laboratory throughout the first decades of the twentieth century.

PROTOZOA AS PROVOCATIVE OBJECTS

The fact that protozoa were objects that provoked the scientific imagination in the late nineteenth and early twentieth centuries arises from their long-standing position at the junctures of well-defined conceptual realms in the life sciences. Since the early decades of the eighteenth century, protozoa were perceived as objects situated at numerous borders in the natural world.[11] Although eighteenth-century naturalists broadly referred to these organisms as "little animals," many were convinced by microscopic observations that protozoa were generated spontaneously from nonliving organic matter and even from living plants. Claims about the spontaneous and vegetative generation of protozoa, made most prominently by Georges Louis Leclerc de Buffon and John Turberville Needham in the 1740s, located protozoa at the juncture between plants and animals and in close proximity to the realm of inorganic matter. The situation was further complicated by Buffon, who speculated that animals and plants are composed of these small, individual, living beings. He conjectured that organisms are a synthesis of infusoria that lose their individuality when they come together to form the whole. Buffon thus also located protozoa at the perplexing boundary between individual being and the "organic parts" that constitute the individual.[12]

[11] As Sherry Turkle maintains, evocative objects fascinate precisely because of their precarious location "betwixt and between" recognized domains: Turkle, *Second Self* (cit. n. 9), pp. 24–25, 31. See also Donald W. Winnicott, "Transitional Objects and Transitional Phenomena: A Study of the First Not-Me Possession," *International Journal of Psycho-Analysis,* 1954, *34:*89–97. As we will see, such borderline positions are transitory, since the domains that these objects straddle and the relationships between them also change over time. For related discussions of boundary objects in the life sciences see S. Leigh Star and James R. Greisemer, "Institutional Ecology, 'Translations,' and Boundary Objects: Amateurs and Professionals in Berkeley's Museum of Vertebrate Zoology," *Social Studies of Science,* 1988, *19:*387–420; Ilana Löwy, "The Strength of Loose Concepts—Boundary Concepts, Federative Experimental Strategies, and Disciplinary Growth: The Case of Immunology," *History of Science,* 1992, *30:*371–396; and Evelyn Fox Keller, "*Drosophila* Embryos as Transitional Objects: The Work of Donald Poulson and Christiane Nüsslein-Volhard," *Historical Studies in the Physical and Biological Sciences,* 1996, *26:*313–346.

[12] On the study of protozoa in the eighteenth century see James Elkins, "On Visual Desperation and the Bodies

The belief that protozoa demarcated the limits of both animality and individuality persisted well into the nineteenth century and was broadly accepted among scholars in the German-speaking world. In 1833, for example, the Romantic naturalist Johann Bernhard Wilbrand claimed that "the first allusion to animal life lies in those simple animal molecules that are called infusion animals." Inspired by the natural philosophy of Friedrich Schelling, Wilbrand aimed to establish a unifying science, under the name of "general physiology," in which comparison of the vital activities of plants and animals would make possible the discovery of the "essence of life." Protozoa occupied the transition point between plants and animals in Wilbrand's scheme; he claimed enthusiastically that protozoa, which were distinguished by their capacity for arbitrary movement, were "the common root for all organs that appear in the further development of animal creation."[13]

Wilbrand's friend and colleague Lorenz Oken believed similarly that the study of infusoria was fundamental to an understanding of the unity of life. Like Buffon, Oken maintained that the flesh of plants and animals alike was composed of "constitutive animals" (*Bestandthiere*) or "primitive animals" (*Urthiere*), the infusoria. When uniting to form the bodies of higher organisms, Oken claimed, these primitive animals surrendered their individuality as they worked in concert for the benefit of a new, and higher, individuality.[14]

As is well known, investigators began to draw on these historical associations between individuality and protozoa in the context of the emerging cell theory. In the 1820s and 1830s botanists such as Pierre Turpin, Franz Meyen, and Matthias Schleiden argued that plants are federations of independent beings or "cells" that, contrary to Oken's claims, retain their individuality within the whole: they can live in isolation and are the source of their own growth and propagation. These ideas culminated in the cell theory advanced in 1839 by Theodor Schwann, who located the vital phenomena not in the "totality of the organism," as was widely assumed, but in the cells themselves. Although specific aspects of the cell theory were subject to considerable revision during the next two decades, Schwann secured the identity of the cell as an independent living being that possessed an "independent vitality"—that is, was capable of growth and securing its own nutrition.[15]

Among those to embrace Schwann's conception of the cell as an entity that possessed independent life was the influential pathologist Rudolf Virchow. In his *Cellular-Pathologie* [*Cellular Pathology*], published in 1858, Virchow, like Schwann, stressed that cells were the fundamental elements of all organic beings. He argued additionally that organisms were collectives of individual entities, since the body of the organism "always represents a kind of social organization of parts . . . in which a number of individual existences are mutually dependent, but in such a way that every element has its own special action." The

of Protozoa," *Representations,* 1992, *40:*33–56; Edward G. Ruestow, *The Microscope in the Dutch Republic: The Shaping of Discovery* (New York: Cambridge Univ. Press, 1996), pp. 260–279; and Marc J. Ratcliff, "Wonders, Logic, and Microscopy in the Eighteenth Century: A History of the Rotifer," *Sci. Context,* 2000, *13:* 93–119.

[13] Johann Bernhard Wilbrand, *Allgemeine Physiologie, insbesondere Physiologie der Pflanzen und Thiere* (Heidelberg: Gross; Vienna: Gerold, 1833), pp. 212–214, iii.

[14] Lorenz Oken, *Die Zeugung* (Bamberg/Wirzburg: Goebhardt, 1805), esp. pp. 22–23; and Klein, "Histoire des origines de la théorie cellulaire" (cit. n. 5), esp. pp. 19–23. To a German reader, Oken would have appeared to have been playing with the German word "*Bestandtheil,*" which means "component" or "element," with his choice of the unusual word "*Bestandthiere.*"

[15] Theodor Schwann, *Microscopical Researches into the Accordance in the Structure and Growth of Animals and Plants,* trans. Henry Smith (London: Sydenham Society, 1842), pp. 191–215; and Klein, "Histoire des origines de la théorie cellulaire."

action that Virchow ascribed to cells was irritability, or the ability to respond to external stimuli. Virchow claimed that irritability was a quality endogenous to the single cell and, he suggested, the source of the social organization that made the existence of higher organisms possible. According to this conception, cells were relational entities similar to higher animals.[16]

The dynamic view of the cell as an individual, championed by Schwann and Virchow among others, facilitated a growing perception that protozoa also straddled the border between cells and organisms. This transformation began in the mid 1840s, when Carl Theodor Ernst von Siebold and Albert von Kölliker reasoned on morphological grounds from cells to protozoa to contend that the latter were unicellular. Siebold furthermore invoked the new cell theory to contend that the analogy drawn by Schwann between plant and animal cells strengthened his own analogy between infusoria and "simple cells."[17]

Such claims about the unicellularity of protozoa had little immediate effect, however, since protozoological researchers remained preoccupied during the next three decades with the ideas of the Berlin-based naturalist Christian Gottfried Ehrenberg, who advocated a doctrine of infusoria as "complete organisms." Ehrenberg's insistence that protozoa possess complete organ systems like those of higher organisms encouraged the implicit assumption that protozoa must be multi- rather than unicellular. At the same time, however, Ehrenberg claimed that protozoa were not only physiologically complete but psychologically endowed as well. While the former interpretation would be overturned in the 1870s, the latter idea would linger, as we will see, until the end of the century.[18]

The reconceptualization of protozoa as unicellular organisms gained new impetus in 1861 when the physiologist Ernst Brücke offered a biological schema of the cell as an elementary organism. In his famous lecture "Die Elementarorganismen" ["The Elementary Organisms"], Brücke maintained that "we must always see in the cell a small animal body and never be allowed to lose sight of the analogies that exist between the cell and the smallest animal forms." In his view, the cell was an element not in the sense that it was an irreducible entity but, rather, in that it was the starting point of future investigations into the complex structures and functions suggested by the analogies with protozoa.[19]

In the 1870s new evidence and arguments culminated in the gradual acceptance that protozoa were indeed unicellular. Beginning in 1873, Ernst Haeckel renounced his earlier views on the matter and proposed that even the behaviorally and morphologically complex ciliates are single-celled organisms, emphasizing, like Siebold before him, the parallels between protozoan and cell nuclei. Three years later, Otto Bütschli cemented this conception of the unicellularity of infusoria with comparative microscopic investigations that further emphasized the physiological parallels between conjugating protozoa and dividing

[16] Rudolf Virchow, *Cellular Pathology as Based upon Physiological and Pathological Histology,* trans. Frank Chance from the 2nd German ed. (1863; Ann Arbor, Mich.: Edwards, 1940), pp. 14, 283–315.

[17] Frederick B. Churchill, "The Guts of the Matter: Infusoria from Ehrenberg to Bütschli, 1838–1876," *J. Hist. Biol.,* 1989, *22:*189–213; and Carl Theodor Ernst von Siebold, *Lehrbuch der vergleichenden Anatomie der wirbellosen Thiere* (Berlin: Viet, 1848).

[18] Mary P. Winsor, *Starfish, Jellyfish, and the Order of Life: Issues in Nineteenth-Century Science* (New Haven, Conn.: Yale Univ. Press, 1976), pp. 28–43; Churchill, "Guts of the Matter"; and Christian Gottfried Ehrenberg, *Die Infusionsthierchen als vollkommene Organismen: Ein Blick in das tiefere organische Leben der Natur* (Leipzig: Voss, 1838). On the critical reception of the unicellular hypothesis of protozoa by T. H. Huxley, in the British context, see Marsha L. Richmond, "T. H. Huxley's Criticism of German Cell Theory: An Epigenetic and Physiological Interpretation of Cell Structure," *J. Hist. Biol.,* 2000, *33:*247–289.

[19] Ernst Brücke, "Die Elementarorganismen," *Sitzungsberichte der Mathematisch-naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften,* 1861, *44:*381–406, on p. 387.

cells. Bütschli's arguments provoked intense debate and investigations, from which a consensus emerged that protozoa are unicellular organisms. The realization that protozoa occupied the organizational juncture between cells and individual organisms laid the groundwork for their use as models of cells, transforming general physiology into a productive experimental enterprise in the late nineteenth and early twentieth centuries. Recognition of the dual status of protozoa as cells and organisms also provoked contemplation of a psychology of cells and protozoa.[20]

TOWARD A CELLULAR PSYCHOLOGY

Leading the enterprise to develop a cellular psychology was Ernst Haeckel, who sketched out his program for psychological research on cells and protozoa at the opening session of the fiftieth meeting of the German Society of Naturalists and Physicians in Munich in 1877. The starting point of Haeckel's program was his philosophy of evolutionary monism, which postulated the unity of mind and matter. In his lecture Haeckel maintained that the obvious consequence of evolutionary theory was that the totality of organic matter was "ensouled" (*beseelt*)—that is, it possessed a psychological life.[21] Recent microscopical investigations, he explained, demonstrated that the seat of this life was the cell. He followed this claim with a catalogue of the most eminent contributions to conceptions of cellular life: he cited Schleiden and Schwann for establishing that the anatomical elements of organisms, the cells, possess an individual and autonomous life (*individuelles selbständiges Leben*); evoking Brücke's "elementary organisms," he contended that cells are "true individuals of the first order"—an idea he had first expressed in his *Generelle Morphologie* [*General Morphology*] in 1866; and he explained that cells were to be seen not as passive building blocks but "as living and active citizens" of the organismic state, as Virchow had shown. This interpretation, he continued, was unquestionably substantiated by investigations of infusoria, amoebas, and other unicellular organisms, since "here we encounter with the single, isolated living cells the same expressions of the psychological life [*Seelenleben*], sensation and representation, will and movement, as with the higher animals, composed of many cells." He concluded his brief outline by specifying further that the cell's *Seelenleben* was seated in the protoplasm and that the molecules of the protoplasm, the *Plastidulae,* were the ultimate factors of psychological life in the organic world.[22]

In a lecture given in Vienna and published in the popular journal *Deutsche Rundschau* in 1878, Haeckel elaborated the ideas that he had sketched out only roughly in his talk in Munich. His article, entitled "Zellseelen und Seelenzellen" ["Psyches of the Cell and Cells of the Psyche"], outlined an evolutionary theory of consciousness that encompassed not only cells and protozoa but also higher animals and human beings. Taking a comparative

[20] Churchill, "Guts of the Matter" (cit. n. 17), pp. 204–211; Ernst Haeckel, "Zur Morphologie der Infusorien," *Jenaische Zeitschrift für Medizin und Naturwissenschaft,* 1873, *7:*516–560; and Otto Bütschli, *Studien über die ersten Entwicklungsvorgänge der Eizelle, die Zelltheilung und die Conjugation der Infusorien* (Frankfurt am Main: Winter, 1876).

[21] Ernst Haeckel, *Die heutige Entwickelungslehre im Verhältnisse zur Gesammtwissenschaft* (Stuttgart: Schweizerbart'sche Verlaghandlung, 1877), p. 12. On the extensive impact of evolutionary theory on the nineteenth-century life sciences see Richards, *Darwin and the Emergence of Evolutionary Theories* (cit. n. 3); Yvette Conry, *L'introduction du darwinisme en France au XIXème siècle* (Paris: Vrin, 1974); and Eve-Marie Engels, *Die Rezeption der Evolutionstheorien im 19. Jahrhundert* (Frankfurt am Main: Suhrkamp, 1995). These sources, however, do not take into consideration the large body of research on protozoa during the period.

[22] Haeckel, *Heutige Entwickelungslehre,* pp. 12–13, 13. Haeckel had been an enthusiastic proponent of the protoplasmic theory of the cell since the late 1860s. On the protoplasmic theory see Gerald L. Geison, "The Protoplasmic Theory of Life and the Vitalist-Mechanist Debate," *Isis,* 1969, *60:*273–292.

approach, he set out to explore "the long ladder [*Stufenleiter*] of the different developmental degrees [*Entwicklungsgrade*] of the animal psyche" in order to illuminate the "origins and boundaries" of psychological life in the animal world. Haeckel again approached his topic from the standpoint of monism and his law of development. The former led him to reject dualist theories that claimed that psychological life was a supernatural phenomenon that could not be explained scientifically.[23] The latter hypothesized a mechanical principle driven by natural selection that caused progressive development at both the species (phylogenetic) and the individual (ontogenetic) levels. This led him to point out the limits of the scientific program of introspection in psychological investigation that became associated with Wundt. Introspective psychology, Haeckel objected, could paint only a one-sided picture of psychological life, namely, that of the fully developed human being, since it failed to access the slow unfolding of the psyche during ontogenesis and phylogenesis. In place of this anthropocentric enterprise, he envisioned a new task for the *Naturforscher*—"the comparative morphology of the psychological organs and the comparative physiology of the psychological functions," carried out with "the most important research instrument"—*Entwicklungsgeschichte.*[24]

The foundation of this vision was again Haeckel's conviction that, as an individual of the first order, every cell has a psyche, or *Zellseele.* The protoplasm of the cell body, together with the substance of the nucleus, he explained, is the "material support" of all psychological life. According to Haeckel, this was perhaps best exemplified by microscopic beings: "the great majority of these protists stay their whole life long on the level [*Formstufe*] of a single and simple cell, and nevertheless this cell undeniably possesses both sensation and voluntary movement." Although there is no evidence suggesting that they possess nerves, muscles, a brain, or sense organs, protists nonetheless display the simple "sensation form" of pleasure and pain and the simple "movement form" of attraction and repulsion.[25]

Haeckel believed that these elementary psychological functions were unconscious. Consciousness, he explained, arises from the "slow and gradual" development of phylogenesis and ontogenesis, during which an increasing "division of labor" takes place among the cellular structures constitutive of the organism. Thus, in more complex lower organisms such as the turbellarians, we find in rudimentary form sense organs, a nervous system, and muscles, the most basic components of a psychological apparatus comparable to that of

[23] Ernst Haeckel, "Zellseelen und Seelenzellen" (1878), rpt. in *Gemeinverständliche Werke,* ed. Heinrich Schmidt, 6 vols. (Leipzig: Kröner; Berlin: Henschel, 1924), Vol. 5, pp. 162–195, on p. 163. Haeckel was referring to the views of Virchow, to be discussed shortly, as well as those expressed by Emil Du Bois-Reymond in his famous "Ignorabimus" lecture, on the problem of consciousness: Emil Du Bois-Reymond, *Über die Grenzen des Naturerkennens: Ein Vortrag auf der zweiten öffentlichen Sitzung der 45. Versammlung Deutscher Naturforscher und Ärzte zu Leipzig am 14. August 1872* (Leipzig: Viet, 1872). See Haeckel, "Zellseelen und Seelenzellen," pp. 174–175; on Virchow see Haeckel, *Freie Wissenschaft und freie Lehre* (1878), in *Gemeinverständliche Werke,* ed. Schmidt, Vol. 5, pp. 196–290, esp. pp. 196–197, 236–247. See also Dietrich von Engelhardt, "Du Bois-Reymond 'Über die Grenzen des Naturerkennens'—eine naturwissenschaftliche Kontroverse im ausgehenden 19. Jahrhundert," *Communicationes de Historia Artis Medicinae,* 1976, *80:*9–25.

[24] Wilhelm Wundt, *Grundzüge der physiologischen Psychologie* (Leipzig: Engelmann, 1874); and Haeckel, "Zellseelen und Seelenzellen," p. 164. On Haeckel's evolutionary morphology and law of development see Lynn K. Nyhart, *Biology Takes Form: Animal Morphology and the German Universities, 1800–1900* (Chicago: Univ. Chicago Press, 1995), esp. pp. 105–277. On his conception of the organic individual see Rinard, "Problem of the Organic Individual" (cit. n. 10).

[25] Haeckel, "Zellseelen und Seelenzellen," pp. 190, 194; see also pp. 191–192. Haeckel believed this was especially evident in the pseudopods of amoebas, which he referred to as "sensitive strings" (*Fühlfäden*) and characterized as rudimentary sense organs.

human beings. Higher psychological functions such as representation, consciousness, and thought emerge only when the inner structures of the organism are developed and specialized further, so that specific cellular structures can be devoted exclusively to psychological processes. By means of these specialized "psyche cells" (*Seelenzellen*), such as the ganglia of the brain, the organization of complex organisms becomes "centralized": the disconnected unconscious activity of the cell psyches is then supplemented by a conscious psychological center, a *Zentralseele,* leading to a unity of the psyche and, at the same time, to consciousness. In higher animals such as dogs and, ultimately, human beings, the unconscious "cell republic," which governs in plants, protists, and other lower organisms, is replaced by a "cell monarchy," where the psyche cells are connected to each other to form an organ that dominates the countless cells of the organism. Haeckel concluded that every living cell has a *cell psyche;* but *psyche cells* are found only in higher animals: "the cell psyche is thus a general [phenomenon], the psyche cell a special phenomenon of organic life."[26]

Haeckel's ideas about cellular psychology were largely eclipsed, however, by the uproar occasioned by the controversial proposal in his 1877 lecture to introduce evolutionary monism in the public schools in the place of religious instruction. Taking a vehement stand against Haeckel at the meeting of naturalists and physicians was Rudolf Virchow, his former mentor. Virchow was fiercely opposed to the dissemination of Haeckel's developmental doctrine in the schools and called for scientists to refrain from that sort of aggressive popularization of scientific doctrines so as not to put at risk the freedom of research and teaching that had only recently been gained in Germany. When he took his turn at the podium, Virchow did not engage directly with Haeckel's proposition for a cellular psychology. Instead he ridiculed a theory that proposed that every cell possessed its own psyche, the product of forces between atoms of carbon, nitrogen, hydrogen, and oxygen. The vindication of such a purely speculative doctrine, he mocked, would require a highly protracted series of scientific investigations. Virchow offered as an alternative his own decidedly anthropological standpoint, querying whether there was really "a scientific need" to extend the domain of mental phenomena to the world of lower beings. His answer was unequivocal: "We have no grounds to say now that the lowest animals possess psychological properties; we find these only in higher and, with certainty, only in the highest animals."[27]

Despite Virchow's contentions and warnings, during the next thirty years numerous scholars undertook the very kind of investigation Haeckel had suggested. Perhaps the most radical attempt to address a part of this agenda—to reduce the phenomena of psychological life to chemical processes—was the mechanistic physiology of Jacques Loeb. Loeb was by no means a Haeckelian, however, since he rejected Haeckel's monistic belief in the autonomous nature of cellular life and, more generally, the metaphysical ruminations that

[26] *Ibid.,* p. 190.

[27] Rudolf Virchow, "Die Freiheit der Wissenschaft im modernen Staatsleben," in *Amtlicher Bericht der 50. Versammlung Deutscher Naturforscher und Ärzte* (Munich: Straub, 1877), pp. 65–78, on p. 75; see esp. pp. 69–70. Haeckel responded to Virchow in 1878 in his book *Freie Wissenschaft und freie Lehre* (cit. n. 23). There he spelled out his theory of the cell soul in greater detail, again presenting it as a development in line with the cell theory of Schleiden, Schwann, and Virchow; he contended, in particular, that "the cellular psychology that I am asking for is only the necessary consequence of the cellular physiology advocated by Virchow" (p. 237). On the debate between Virchow and Haeckel see Dietrich von Engelhardt, "Virchow et Haeckel et la liberté de la science," in *Médecine et philosophie à la fin du XIXème siècle,* ed. Jacques Poirier and Jean-Louis Poirier (Val de Marne: Univ. Paris XII, n.d.), pp. 117–125. More broadly, see John R. Baker, *The Controversy on Freedom in Science in the Nineteenth Century* (Oxford: Society for Freedom in Science, 1962).

characterized the German scholar's theorizing.[28] Rather, it was Max Verworn whose *Psycho-physiologische Protistenstudien* [*Psychophysiological Protist Studies*]—dedicated to his teacher, Haeckel, and ridiculed by Loeb—helped to define the experimental research program that shall occupy us in the remainder of this essay.

MAX VERWORN'S PSYCHOPHYSIOLOGY OF PROTISTS AND THE UNITY OF NATURE

Max Verworn studied under Emil Du Bois-Reymond, Rudolf Virchow, Ernst Haeckel, and William Preyer, among others, before publishing his *Psycho-physiologische Protistenstudien* in 1889. Verworn initiated his career with a study of the freshwater bryozoans, a group of colonial invertebrates that possess exoskeletons, for which he earned his Ph.D. in Berlin in 1887 under the direction of the zoologist Franz Eilhard Schulze. Even at this early date, Verworn's concerns encompassed the metaphysical as well as the physiological, and his adherence to "psycho-monism"—his belief that all phenomena of the physical and psychological worlds share a single underlying nature—began to take firm shape. In his thesis Verworn argued that neither a nervous system nor sense organs are necessary for the existence of psychological life. He subsequently maintained that the science of psychology could be extended beyond the realm of beings that possess a well-defined nervous system—that it should account for considerably more than humans and other higher organisms (see Figure 1).[29]

Guided by these views, Verworn initiated psychological research on the movements of protozoa while in Berlin, work he continued when he moved to Jena in 1887. In the same year that he published his extensive *Psycho-physiologische Protistenstudien,* Verworn was awarded an M.D. for a shorter study of the effects of electric current on the movement of protozoa. Although his thesis was directed by the young physiologist Wilhelm Biedermann, Verworn's research drew its chief inspiration from Haeckel and from Biedermann's predecessor, William Preyer (1841–1897), who had studied in Paris with Claude Bernard and occupied the chair of physiology at Jena until 1888. Despite his primary focus on physiology, Preyer had engaged in considerable psychological research earlier in his career, publishing a pioneering work in developmental psychology, *Die Seele des Kindes* [*The Mind of the Child*], in 1882. In 1883 Preyer published *Elemente der allgemeinen Physiologie* [*Elements of General Physiology*], which, like his psychological work and the ideas of his close colleague, Haeckel, was grounded in an evolutionary framework.[30]

[28] On Loeb see Philip J. Pauly, *Controlling Life: Jacques Loeb and the Engineering Ideal in Biology* (New York: Oxford Univ. Press, 1987). See also Donald Fleming, "Introduction," in Jacques Loeb, *The Mechanistic Conception of Life,* ed. Fleming (Cambridge, Mass.: Belknap, 1964), pp. vii–xli; and Charles Rasmussen and Rick Tilman, *Jacques Loeb: His Science and Social Activism and Their Philosophical Foundations* (Philadelphia: American Philosophical Society, 1998). On Loeb and general physiology see Pauly, "General Physiology and the Discipline of Physiology" (cit. n. 6).

[29] Max Verworn, *Beiträge zur Kenntnis der Süsswasser-Bryozoen,* Ph.D. thesis (Berlin: Gustav Schade/Otto Francke, 1887), p. 48. On Verworn's psychomonism see Verworn, *Naturwissenschaft und Weltanschauung* (Leipzig: Barth, 1904); and Verworn, *Prinzipienfragen in der Naturwissenschaft* (Jena: Fischer, 1917). On Verworn see Raimund Wüllenweber, "Der Physiologe Max Verworn" (M.D. thesis, Univ. Bonn, 1968); his psycho-monism is discussed on pp. 24–29.

[30] Max Verworn, *Die polare Erregung der Protisten durch den galvanischen Strom,* M.D. thesis (Bonn: Strauss, 1889); the thesis was also published in *Archiv für die Gesammte Physiologie des Menschen und der Thiere,* 1889, *46:*1–36. William T. Preyer, *Die Seele des Kindes: Beobachtungen über die geistige Entwicklung des Menschen in den ersten Lebensjahren* (Leipzig: Grieben, 1882); and Preyer, *Elemente der allgemeinen Physiologie: Kurz und leichtfasslich dargestellt* (Leipzig: Grieben, 1883). An English translation of the developmental psychology volume appeared five years later: Preyer, *The Mind of the Child,* trans. H. Brown, with an introduction by G. Stanley Hall (New York: Appleton, 1888–1889). On Preyer see Siegfried Jaeger, "Origins of Child

Figure 1. *Max Verworn, 1887. Courtesy of the Museum für Naturkunde der Humboldt-Universität zu Berlin, Historische Bild- u. Schriftsammlungen, Zool. Mus., Signature B I/1277.*

Eager to acknowledge his intellectual debts and to document his own scholarly pedigree as an evolutionist, Verworn dedicated his *Protistenstudien* "with sincere gratitude" to his "dear teacher Ernst Haeckel." In the dedicatory preface to his mentor, he wrote: "When I approached my zoological training under your direction at the zoological institute at Jena, it was, from the beginning, the life of the lowest organisms which aroused my interest to the highest degree. Because here, on the lowest level of life generally, within the frame of a single cell, all phenomena of life that we observe in the highest organisms could already be found in their simplest form." Much like Haeckel, Verworn emphasized that in order to understand all the phenomena of life—including psychological phenomena—it was necessary to "go back to the elementary organisms." Specifically, he explained, it was

Psychology: William Preyer," in *Problematic Science,* ed. Woodward and Ash (cit. n. 4), pp. 300–321; and Georg Eckardt, Wolfgang G. Bringmann, and Lothar Sprung, eds., *Contributions to a History of Developmental Psychology: International William T. Preyer Symposium* (Berlin: Mouton, 1985).

Haeckel's idea of a "cell psyche" that inspired his own interest in the psychological processes of animals, particularly his focus on the "psychological life of the lowest organisms." He elaborated in the introduction, a few pages later, that "it is impossible to come to any insight in this direction, as long as the only objects of investigation are the complicated psychological processes in human beings and the higher animals." Just as in zoological morphology one must turn to the lower animals to find "the more original and simple forms, . . . the same observation holds of course true for the psychological phenomena, and thus research on the psychological life of lower animals indeed must spread light over the psychology of the higher animals and of human beings."[31]

Verworn initiated his investigations with what he called "pure observations" of the spontaneous movements and the life activities of the organisms, which were meant to provide a foundation for the two experimental methods that were the focus of the book: investigations of behavior in protozoa under systematically varied artificially induced conditions such as light, heat, and electricity; and vivisection experiments—procedures requiring, as he underlined, much patience and skill—that sought to localize physiological and psychological functions in the protists. In both cases he transferred the techniques of electrophysiological stimulation as they were used in the laboratory of Du Bois-Reymond onto his microscopic stage, thus transforming the microscope—an instrument traditionally used for observational practices—into a physiological laboratory *en miniature.*[32]

Although generally inspired by the ideas of Haeckel, Verworn's investigations were more concretely modeled on Preyer's psychological studies of the development of movements in children. The rationale for this approach, he explained, was that the movements of protozoa constituted the "only objective expressions of the subjective processes" of the mental life of nonhuman beings; in other words, in the absence of the study of movements, there would be no grounds at all for attributing psychic processes to protozoa. In his psychological investigations Verworn distinguished between spontaneous movements, those movements occurring independently of experimental intervention, and what he termed "stimulation movements" (*Reizbewegungen*), that is, movements that immediately follow the onset of experimental stimuli, such as heat, electricity, or magnetism. Throughout much of the text he recounted the diverse methods by which he produced stimulation movements; for example, he caused the organisms to arrange themselves like "iron filings . . . distributed on a sheet of paper held over a horseshoe magnet" when he placed two pointed electrodes in the opposite sides of a drop of water containing paramecia. Verworn typically depicted these movements in large groups of organisms, focusing on the final state in which their actions resulted collectively in a common orientation (see Figure 2). Stimulation movements, he explained, were pure "reflex movements"—a term he borrowed from Preyer—since, in general, protozoa "respond to every stimulus always in the same way, with a machine-like lawfulness and without the slightest deviation." He concluded that even though heliotropic, thermotropic, and galvanotropic behaviors often give the appearance of adaptive or purposeful action, they bear no relation to higher psychological processes. They are not conscious or voluntary acts.[33]

[31] *Verworn, Psycho-physiologische Protistenstudien* (cit. n. 7), pp. v, vi, 3.

[32] *Ibid.,* pp. 27–34, 34–130, 156–183.

[33] *Ibid.,* pp. 19, 117, 137, 136–140. Preyer's *Die Seele des Kindes* was based on daily observations of his own son that he undertook over several years. The book is divided into three parts dedicated to the development of the senses, the will, and the intellect. According to Preyer, movements are direct expressions of the will. Impulsive movements are the earliest stage in the development of the will. They are followed by the emergence of reflexive, instinctive, and imitative movements. During the course of development, movements become increasingly con-

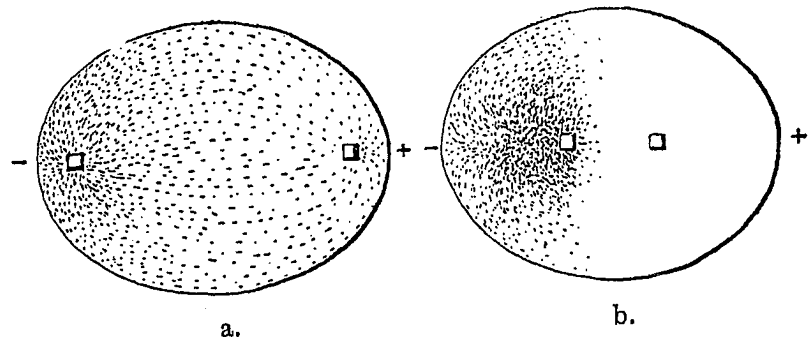

Figure 2. *Reaction of paramecia to electrical current, referred to as "galvanotropism." From Max Verworn,* Psycho-physiologische Protistenstudien: Experimentelle Untersuchungen *(Jena: Fischer, 1889), p. 118.*

In addition, however, Verworn maintained that the spontaneous movements of protozoa could not be regarded as expressions of will or consciousness. He argued that such actions are either highly limited and repetitive—for example, the pulsation of vacuoles in the bodies of protozoa—and hence should be seen as "automatic"; or they are random—as in the sudden bursts of thrashing of peristomal cilia in many ciliates—and should be considered "impulsive"—another term borrowed from Preyer's analysis of movement in children. Even the most complicated spontaneous activities associated with nutrition, conjugation, and the construction of a protective shell, as in the amoeboid *Difflugia,* he concluded, were not willful or conscious movements. These "unconscious voluntary processes" (*unbewusste Willensvorgänge*) did not imply the workings of choice but were merely combinations of stimulus, impulsive, and automatic movements.[34]

Verworn found these interpretations to be supported by his investigations of sensory functions in protozoa, which proved to be minimally organized. He contended that reactions to light occurred equally in those protozoa that do not possess the pigment spots described by some naturalists as "eyes" or "sense organs" as in those that do. He also found that—with the exception of flagella and cilia, which are highly sensitive to mechanical stimuli—every part of the protoplasm is equally sensitive to mechanical, chemical, and electromagnetic stimuli and heat and that protozoa exhibit no differentiation of specific organs sensible to these stimuli. Even in the case of "the most highly developed protists," the ciliates, Verworn found that there are no "sensible elements" for light sensation; and in those lesser-developed protozoan groups that do possess such sensible elements, they are only sufficiently evolved to distinguish between brightness and darkness. In either case, without a differentiated sense organ for light perception, a "representation of the ego" is highly imperfect if not impossible in protozoa, and out of this "imperfection of an ego-representation [it] follows . . . with necessity that conscious psychic processes . . . cannot yet exist."[35]

At this point it might have seemed that Verworn's study of an explicit *psycho*physiology

nected to representations, and "deliberate (*überlegte*) movements" become possible. These indicate the existence of a "pure will" in the child, which is the basis of his or her intentional behavior. See Preyer, *Seele des Kindes* (cit. n. 30), pp. 119–218.

[34] Verworn, *Psycho-physiologische Protistenstudien,* pp. 140–143, 155–156.

[35] *Ibid.,* pp. 125–130, 144–146.

of protozoa was in danger of collapse. From the perspective of a psychology focused on the will, consciousness, and the ego, it indeed would have been difficult to understand how his studies of protozoa contributed to psychology, since they provided no evidence of or insights into any of these “higher” psychological processes. Yet Verworn’s conclusion pointed in exactly the opposite direction: he concluded instead that every part of the protozoan body possessed psychological properties. Evidence for this interpretation emerged in the final part of his study, where he employed microvivisection techniques to produce denucleated body segments whose spontaneous and stimulus movements proved that the protozoan nucleus was not the center of psychological function, as some researchers had suspected. In addition, in each of the species he tested Verworn found that the denucleated protoplasmic pieces he created with his tiny scalpel had the same responses to various experimental stimuli as their uninjured counterparts (see Figure 3). A final experiment showing that the coordinated sweeping actions of the peristomal cilia broke down at the point of an incision led Verworn to reintroduce the metaphors of civil society employed by his teacher Rudolf Virchow thirty years earlier. Whereas Virchow had drawn on the relations between free citizens in a liberal state to describe the relations between cells in the organism, Verworn employed the notion to characterize relations between each tiny “protoplasmic part” within the microscopic single-celled animal body: “One may compare the whole protist body to a large gathering of people, where each person corre-

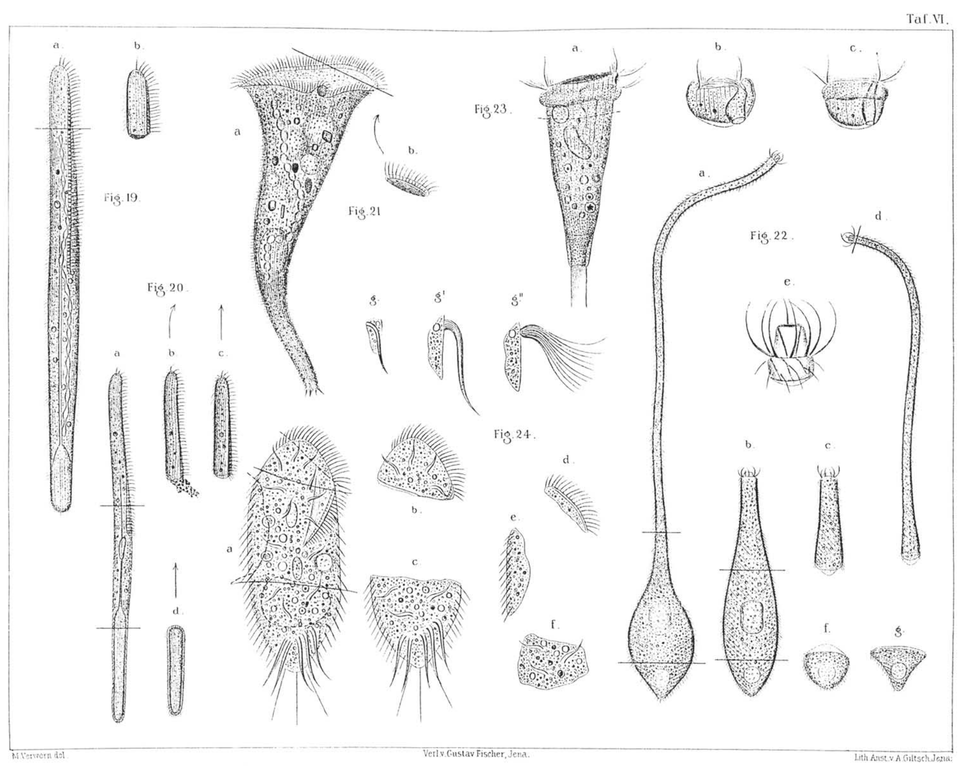

Figure 3. *Microvivisection experiments in different protozoa. The straight lines indicate where the organism was cut. From Max Verworn,* Psycho-physiologische Protistenstudien: Experimentelle Untersuchungen *(Jena: Fischer, 1889), Plate 6.*

sponds to a small part of protoplasm. The decisions of the gathering are the total movements of the whole body. . . . But just as in the gathering every person is an autonomous individual with its own opinion, every small part of protoplasm possesses its autonomy." Convinced by these experimental results that unveiled a "republican constitution" (*republikanische Verfassung*) of the elementary parts of the protozoan body, Verworn ultimately concluded that protozoa possessed elementary sensations and representations—albeit unconscious ones—in addition to the unconscious processes of reflexive, automatic, and impulsive movements that he had observed previously. As he summarized it, he had found that, indeed, "every elementary part of protoplasm has its own autonomous psyche." In other words, Verworn located individuality not on the level of the protozoan as a whole but in its protoplasmic parts.[36]

Yet the connection between these very rudimentary psychic properties and the conscious acts of higher organisms remained precariously unexplained. In tackling this problem in the final pages of his text, Verworn enthusiastically adopted the principles of Haeckel's controversial 1877 lecture, likewise transforming his own psychophysiological protist studies into a simultaneously evolutionary and chemically based "molecular psychology." He thus maintained that "the moving cause of the protist body lies in the molecular processes of its elementary parts, and out of them the psyche of the higher animals and human beings has developed." According to Verworn, movements in protozoa were caused by molecular processes within and among the protoplasmic parts, which represented the rudimentary functions of a nervous system. These same molecular processes, however, were the source from which the nervous systems of metazoans and, eventually, humans had evolved; consequently, the psychological processes of the lowest and highest beings were united in the same chemical foundations. Thus while the movements and sensibility of the protoplasmic microorganisms were fundamental psychological phenomena in their own right, they were also the evolutionary precursors of the higher psychological processes observed in higher organisms. It is from this perspective of a chemically and evolutionarily grounded psychophysiology that Verworn, much like his mentor Ernst Haeckel, turned to the lowly protozoan to demonstrate the unity of all psychological, and indeed all natural, phenomena.[37]

ALFRED BINET AND THE "PSYCHIC LIFE" OF MICROORGANISMS

Verworn was neither the first nor the only scholar seriously engaged in studying the psychophysiology of protozoa; two years earlier, in 1887, Alfred Binet had published a study on the "psychology of proto-organisms." His results appeared in two parts in Théodule Ribot's *Revue Philosophique* [*Philosophical Review*], the leading French journal for psychology at that time. In "La vie psychique des micro-organismes" ["The Psychic Life of Microorganisms"] Binet presented microorganisms as important objects for psychological research. At the outset, he explained that many "interesting facts" about the "psychic life" of microorganisms had been collected by scholars over the years but that they had been

[36] *Ibid.,* pp. 187–188, 190, 192; cf. Virchow, *Cellular Pathology,* trans. Chance (cit. n. 16), pp. 283–315. On Virchow see Frederick B. Churchill, "Rudolf Virchow and the Pathologist's Criteria for the Inheritance of Acquired Characteristics," *J. Hist. Med. Allied Sci.,* 1976, *31:*117–148, esp. pp. 130–132; and Duchesneau, *Genèse de la théorie cellulaire* (cit. n. 5), pp. 301–323. On the ideological aspects of Virchow's views of the organism as a cell state see Paul Weindling, "Theories of the Cell State in Imperial Germany," in *Biology, Medicine, and Society, 1840–1940,* ed. Charles Webster (Cambridge: Cambridge Univ. Press, 1981), esp. pp. 116–120; and Renato Mazzolini, *Politisch-biologische Analogien in Frühwerk Rudolf Virchows* (Marburg: Basilisken-Presse, 1988).

[37] Verworn, *Psycho-physiologische Protistenstudien,* pp. 202, 200–207, 212–213.

insufficiently understood and discussed as psychological phenomena. Since the data were dispersed in monographs and journals of all kinds, "where the psychologist does not think of looking for them," he intended to familiarize readers of the *Revue* "with a part of these treasures" and, as a consequence, to make a whole field of new topics accessible to psychological research. Binet's two-part article was revised and published as part of a book, *Études de psychologie expérimentale,* in 1888 and translated into English in 1889 and into German in 1892.[38]

In his review Binet commented on the work of many of the leading naturalists and microscopic anatomists who had recently engaged in protozoological study. In addition to the publications of Theodor Engelmann, Otto Bütschli, René-Édouard Claparède and Johannes Lachmann, and Friedrich Stein, among others, he quoted extensively from the publications and even the personal communications of Édouard-Gérard Balbiani and Émile Maupas. Balbiani, who was named professor of comparative embryology at the Collège de France in 1874, was a prolific researcher in many fields of study. His lifelong interest, however, was reproduction in infusoria. An adherent of the French tradition of general physiology, Balbiani introduced Binet to protozoan research. Beginning in 1887, Binet attended Balbiani's lectures and took up research in his laboratory, devoting himself both to the studies that culminated in his articles on microorganisms and to investigations of anatomical and physiological aspects of the subintestinal nervous system in insects that would result in his 1894 doctoral thesis.[39]

The primary contention of "La vie psychique des micro-organismes" was that single-celled microorganisms indeed have a psychological life. This conviction was grounded in at least two assumptions. The first derived from both Binet's evolutionary perspective and his exposure to general physiology under Balbiani. Binet argued that there was a continuous developmental series reaching from human beings down to the most elementary forms of life. As a consequence, the psychological properties and processes that were known from the study of humans could also be expected in the lowest living beings, albeit in elementary form. He made this assumption explicit in the preface "written especially for the American Edition" of his book, where he criticized the British scholar George Romanes

[38] Binet, "Vie psychique des micro-organismes" (cit. n. 7), pp. 450, 449. For the revised French version see Alfred Binet, *Études de psychologie expérimentale* (Paris: Doin, 1888), pp. 87–237. For the translations see Binet, *The Psychic Life of Micro-organisms: A Study in Experimental Psychology,* trans. Thomas McCormack (London: Longmanns, Green, 1889); and Binet, *Das Seelenleben der kleinsten Lebewesen,* trans. W. Medicus (Halle: Schwetschke'scher, 1892). On Binet see François Louis Bertrand, *Alfred Binet et son oeuvre* (Paris: Alcan, 1930); Edith J. Varon, "The Development of Alfred Binet's Psychology," *Psychological Monographs,* 1935, *46:*1–129; Theta H. Wolf, *Alfred Binet* (Chicago/London: Univ. Chicago Press, 1973); and Raymond E. Fancher, "Alfred Binet, General Psychologist," in *Portraits of Pioneers in Psychology,* ed. George A. Kimble and Michael Wertheimer, 3 vols. (Washington, D.C.: American Psychological Assoc., 1991–1998), Vol. 3, pp. 67–83. For a bibliography of Binet's extensive publications see Varon, "Development of Alfred Binet's Psychology," pp. 121–129.

[39] Alfred Binet, *Contribution à l'étude du système nerveux sous-intestinal des insectes,* Ph.D. thesis (Paris: Alcan, 1894). Claude Bernard greatly admired Balbiani, putting him in charge of the histological section of the laboratory of general physiology at the Muséum d'Histoire Naturelle in 1867 before playing a major role in his election to the Collège de France seven years later. On Balbiani see L. F. Henneguy, "E. G. Balbiani (1823–1899)," *Archives d'Anatomie Microscopique,* 1900, *3:*1–31. See also Bernard, *Rapport sur les progrès et la marche de la physiologie générale* (cit. n. 5), pp. 102–103, which details Bernard's positive views of Balbiani's scholarship and his contribution to the development of general physiology ca. 1867. Binet maintained close ties with Balbiani, who was his father-in-law as well as his mentor. A year after Binet published his article on the psychic life of microorganisms, the *Revue Philosophique* also published his report of Balbiani's lectures on generation and heredity at the Collège de France; see E.-G. Balbiani, "Les théories modernes de la génération et de l'hérédité," *Rev. Phil. Fr. Étrang.,* 1888, *25:*529–559.

for denying that psychological properties exist in microorganisms. Binet argued: "If the existence of psychological phenomena in lower organisms is denied, it will be necessary to assume that these phenomena can be superadded in the course of evolution, in proportion as an organism grows more perfect and complex. Nothing could be more inconsistent with the teachings of general physiology, which shows us that all vital phenomena are previously present in non-differentiated cells." Binet bolstered his argument by pointing out that many other investigators who studied protozoa supported his view, among them his mentor Balbiani, the naturalist Karl Möbius, and Max Verworn. In doing so he implied his adherence to monism, but he did not make such views central to his arguments.[40]

In addition, Binet argued that it was insufficient to ascribe the actions and capabilities of protozoa to simple cellular irritability. He cautioned that "even on the very lowest rounds of the ladder of life, psychic manifestations are very much more complex than is usually believed." Among the simplest living beings, he explained, "we find manifestations of an intelligence which greatly transcends the phenomena of cellular irritability." Binet thus focused his study not, as Verworn did, on the two elements widely agreed to constitute the "life of relation" of an irritable cell—that is, its sensibility and reactions to the external world—but on more complex phenomena. He provided a general overview of the most important groups of protozoa, then moved on to discuss their motor organs, the "diffused nervous system" contained in their protoplasm, and the "eyes" or "ocular spots" that he thought constituted the sense organs of many species.[41] He next examined in more detail the psychological activities associated with nutrition and fecundation, before concluding with a discussion of the physiological role played by the nucleus in the organisms' psychological functions.

With respect to feeding, Binet was primarily interested in what he referred to as "animal nutrition," the introduction of food into either a temporary or a permanent mouth. He claimed that the movements constituting microorganisms' search for food are "not simple movements," since, among other things, the protozoan must "guide itself" to avoid obstacles or move them aside, direct its prehensile organs toward the objects it encounters, and distinguish food from worthless materials. In some species the protozoan selects only certain types of food, meaning that it exercises choice. Binet concluded from observing these actions that "the movements in the free infusoria show all the characteristics of voluntary movements." He found this "voluntarism" to be especially evident in the process of catching living prey. Although he acknowledged the undesirability of anthropomorphic language in such studies, he nonetheless used it freely throughout the text. Thus, to demonstrate his point, he referred to a "hunt" in which "attack" and "defense" organs are used, such as when the *Didinium* "fires" its rodlike trichocysts at its "victim." In other cases he

[40] Binet, *Psychic Life of Micro-organisms,* trans. McCormack (cit. n. 38), pp. iv–v, v. For Romanes's response to Binet's criticisms see George John Romanes, "The Psychic Life of Micro-organisms," *Open Court,* 1889, *98:*1715–1719. Although Binet was familiar with Haeckel's zoological studies and his ideas for a cellular psychology, it is not clear to what extent he shared his monistic beliefs. Even Binet's more philosophical studies published after the turn of the century are not very instructive. He does describe himself as a "monist" in his article "Esprit et matière," but this seems to refer more to an experiential monism of the sort advocated by Ernst Mach than to a Haeckelian worldview. See Alfred Binet, "Esprit et matière," *Bulletin de la Société Française de Philosophie,* 1905, *5:*73–101, esp. p. 86; Binet, "Cerveau et pensée," *Archives de Psychologie,* 1907, *6:*1–26; and Binet, *L'âme et le corps* (Paris: Flammarion, 1905). For comments on these texts see Wolf, *Alfred Binet* (cit. n. 38), pp. 339–347. On evolutionism and *Entwicklungslehre* in France more generally see Conry, *Introduction du Darwinisme en France* (cit. n. 21).

[41] Binet, *Psychic Life of Micro-organisms,* trans. McCormack, p. 3; and Binet, "Vie psychique des micro-organismes" (cit. n. 7), pp. 450–470.

found that microorganisms unite in "troops" to attack other animals, often much bigger than themselves, suggesting that they possess a rudimentary social organization.[42]

Although Binet agreed that morphological and physicochemical conditions were important determinants of such activities, he was convinced that some sort of intelligence that could not be reduced to the phenomena of irritability also came into play. The goal-directed movements of protozoa presupposed an organized connection between certain stimuli and certain movements in their protoplasm. He concluded that this connection was psychological in nature, since "to explain the physical nature of this connection seems to be totally impossible."[43]

Binet's arguments about the process of fecundation in microorganisms were similarly antireductionist. Here, he relied extensively on Balbiani's claims and related observations that ciliates reproduce sexually by mating followed by internal fertilization. From this and related material he concluded that conjugation in protozoa was not purely mechanical but was, rather, a psychological phenomenon. He maintained that the frenzy of interactions between protozoa preceding sexual intercourse showed clearly that they were moving voluntarily and consciously. The coupling itself was of special interest, because there "the psychologist can admire the precision with which the two individuals take the attitude necessary for fecundation."[44]

Despite his obvious fascination with the psychological life of microorganisms, Binet did not pursue the topic further. Like his early studies on suggestibility and transfer phenomena, carried out with the psychiatrist Charles Féré at the Salpêtrière, his investigations of microorganisms met with criticism. This time the objections came from Charles Richet, professor of physiology at the Paris Medical Faculty. Their dispute, which was aired in the pages of the *Revue Philosophique,* centered on the appropriateness of using protozoa as models of cells, since, as Richet claimed, they are decidedly not simple. Richet insisted that only "homogeneous" cells, cells that are in no way differentiated, are appropriate objects for an "elementary psychology of the cell"—to which Binet retorted that no such thing as a "homogeneous" cell exists.[45] Whether or not Binet felt that he had persuaded Richet or anyone else, he was not a scholar to remain in any one intellectual space for long. After completing these investigations, he turned to his studies of the nervous system in insects and then to psychological chronometry, before eventually focusing on the psychology of reasoning and child psychology (see Figure 4).[46] As will be discussed later in this essay, we believe that Binet's psychological studies of unicellular organisms played an important role in shaping this important final stage of his research career.

[42] Binet, "Vie psychique des micro-organismes," pp. 479–480, 489; for another example of anthropomorphic language see p. 583.

[43] *Ibid.,* p. 585.

[44] *Ibid.,* pp. 585–587, p. 587.

[45] Charles Richet, "La vie psychique des micro-organismes," *Rev. Phil. Fr. Étrang.,* 1888, *25:*219–220; and Alfred Binet, "Réponse à M. Ch. Richet," *ibid.,* pp. 220–224. On Binet's conflict with the Nancy school and his debate with the Belgian psychophysicist Joseph Delboeuf see Wolf, *Alfred Binet* (cit. n. 38), pp. 40–78; on the Nancy school and the Charcot school more generally see Henri F. Ellenberger, *The Discovery of the Unconscious: The History and Evolution of Dynamic Psychiatry* (New York: Basic, 1970), pp. 85–101.

[46] It is in the latter context that Binet developed the intelligence scale for which he is most famous. On the Binet scale of intelligence and its subsequent history see Stephen Jay Gould, *The Mismeasure of Man* (New York: Norton, 1981), pp. 146–233. When Binet started to work in the laboratory for physiological psychology at Sorbonne University in Paris in 1889, he referred to Wundt's Leipzig laboratory as one of the models for the institution. The research carried out by Binet at the Sorbonne did not closely follow Wundt's research program, but contributed instead to the further development of Binet's own psychology. See Jacqueline Carroy and Henning Schmidgen, "Psychologies expérimentales: Leipzig–Paris (1890–1910)," *Max Planck Institute for the History of Science Preprint 206,* 2002.

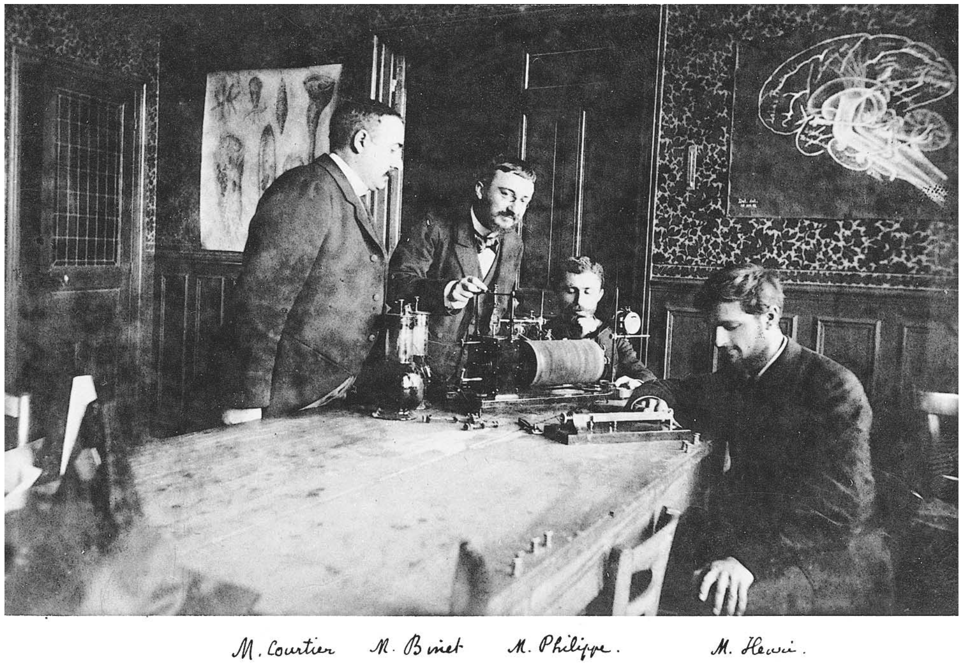

Figure 4. *Alfred Binet with collaborators in his laboratory at Sorbonne University, circa 1890. In the background to the left and right of the experimenters are wall charts depicting infusoria and the human brain, respectively. Photograph courtesy of Régine Plas, Paris, and reproduced by the Service Photographique des Archives Nationales, Paris, Signature Iy 101-2.*

HERBERT SPENCER JENNINGS AND THE METHOD OF TRIAL AND ERROR IN LOWER ORGANISMS

In autumn 1896, approximately ten years after Verworn and Binet initiated their studies of protozoa, the American zoologist Herbert Spencer Jennings launched his own investigations of the behavior of unicellular organisms in Verworn's laboratory in Jena. Jennings took up these studies during a year of postdoctoral study funded by a travel fellowship awarded by Harvard University, where he had just completed his Ph.D. under the cytologist Edward L. Mark. His thesis was a classic cell-lineage study of the rotifer *Asplanchna* that traced the early development of this microscopic metazoan from fertilization through gastrulation. As was characteristic of this genre of embryological research, Jennings's investigation was concerned with the processes determining cell cleavage and early development and required advanced microscopy and observational skills (see Figure 5).[47]

[47] For the doctoral thesis see Herbert S. Jennings, "The Early Development of *Asplanchna Herrickii de Guerne:* A Contribution to Developmental Mechanics," *Bulletin of the Museum of Comparative Zoology,* 1896, *30:*1–117. On cell-lineage studies see Jane Maienschein, "Cell Lineage, Ancestral Reminiscence, and the Biogenetic Law," *J. Hist. Biol.,* 1978, *11:*129–158; and Maienschein, "Shifting Assumptions in American Biology: Embryology, 1890–1910," *ibid.,* 1981, *14:*90–113. On Jennings see T. C. Schneirla, "Herbert Spencer Jennings: 1868–1947," *American Journal of Psychology,* 1947, *60:*447–450; T. M. Sonneborn, "Herbert Spencer Jennings, 1868–1947," *Biographical Memoirs of the National Academy of Sciences,* 1975, *47:*143–223; and Sharon Kingsland, "A Man out of Place: Herbert Spencer Jennings at Johns Hopkins, 1906–1938," *American Zoologist,* 1987, *27:*807–817.

Figure 5. *Herbert Spencer Jennings, 1926. Courtesy of the American Philosophical Society.*

During his studies Jennings formulated a perspective on biological phenomena that focused on the internal regulatory response of the organism or cell to external stimuli rather than on the inanimate "effects" of those stimuli themselves. Contributing significantly to the formation of Jennings's views, which he would retain throughout his career, were the investigations of the embryologist Wilhelm Roux, who also trained at Jena. Although Roux is best known for his insistence on using experimentation to analyze biological processes as mechanical phenomena, reduced to the simplest terms possible, he employed these methods, which he referred to as *Entwicklungsmechanik* ("developmental mechanics"), to address questions about the functional adaptation of internal factors of cell development. Though he did not immediately adopt the experimental component of Roux's program of *Entwicklungsmechanik,* Jennings embraced his functional approach in his own studies of early development.[48]

[48] On Roux and the history of *Entwicklungsmechanik* see Frederick B. Churchill, "From Machine-Theory to Entelechy: Two Studies in Developmental Teleology," *J. Hist. Biol.,* 1969, *2:*165–185; Churchill, "Chabry, Roux,

Also providing important resources for Jennings's conception of functional adaptation were the investigations of another young Jena-trained embryologist, Curt Herbst. In 1894 and 1895 Herbst applied the ideas of stimulus physiology to animal morphogenesis to argue that "just as free-moving organisms [such as plants and protozoa] are influenced in the direction of their movement by outer agents, so also do independent tissues respond to certain directional stimuli." In his Ph.D. thesis Jennings seized on Herbst's analogy between lower organisms and cells in a developing organism to argue that the direction of cell cleavage in early development resulted from the reaction of the dividing cell to a form-determining stimulus.[49]

Because his Ph.D. investigations were largely descriptive, Jennings aimed to expand them during his postdoctoral studies into an experimental inquiry that would illuminate how embryological cells responded to stimuli during development. In Max Verworn's general physiology laboratory he planned to investigate the behavior of free-living cells—that is, protozoa—as a model that might shed light on the actions of groups of embryological cells.[50]

Jennings abandoned his original goal, however, when he became engrossed with the behavioral responses of unicellular organisms as scientific phenomena in their own right. Once in Jena, he outlined an experimental research program that aimed to build a comprehensive picture of the typical activities of the individual unicellular organism. These included their reactions and the interplay of reactions under ordinary circumstances of multiple and interacting stimuli and changing responses to fluctuating environmental conditions and physiological states. At the same time, Jennings took advantage of the many intellectual resources available in Jena: he attended Verworn's lectures on general physiology, Wilhelm Biedermann's lectures on human physiology, Otto Liebmann's lectures on psychology, which impressed him greatly, and a few of Haeckel's lectures—until he lost interest and stopped attending, claiming that they were too popular and general in nature. His attitude toward Haeckel was likely prompted by the German zoologist's neglect of adaptation as an evolutionary cause, which served as the foundation of Jennings's own early preoccupation with the adaptive capacity of organisms.[51]

Jennings's postdoctoral research studies resulted in a series of ten articles between 1897 and 1902, eight of which he published in the *Journal of Physiology* and the *American Journal of Physiology.* Jennings presented his work as a contribution to both general physiology and comparative psychology, yet his choice of publishing venues suggests the importance to him of building his investigations on a physiological foundation. These articles

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and the Experimental Method in Nineteenth-Century Embryology," in *Foundations of Scientific Method: The Nineteenth Century,* ed. Ronald N. Giere and Richard S. Westfall (Bloomington: Indiana Univ. Press, 1973), pp. 161–205; Reinhard Mocek, *Wilhelm Roux—Hans Driesch: Zur Geschichte der Entwicklungsphysiologie der Tiere ("Entwicklungsmechanik")* (Jena: Fischer, 1974); and Jane Maienschein, "The Origins of *Entwicklungsmechanik,*" in *A Conceptual History of Modern Embryology,* ed. Scott F. Gilbert (Baltimore: Johns Hopkins Univ. Press, 1991), pp. 43–61.

[49] Curt Herbst, "Ueber die Bedeutung der Reizphysiologie für die kausale Auffasung von Vorgängen in der tierischen Ontogenese: I," *Biologisches Centralblatt,* 1894, *14:*721–745, 753–772, 792–805, 817–831, 849–855; and Herbst, "Ueber die Bedeutung der Reizphysiologie für die kausale Auffasung von Vorgängen in der tierischen Ontogenese: II," *ibid.,* 1895, *15:*657–666, 689–697, 727–744, 753–771, 800–810.

[50] Herbert S. Jennings to Joseph Brennemann, 10 May 1896, Herbert Spencer Jennings Papers, American Philosophical Society, Philadelphia, Pennsylvania.

[51] Herbert S. Jennings, "Studies on Reactions to Stimuli in Unicellular Organisms, I: Reactions to Chemical, Osmotic, and Mechanical Stimuli in the Ciliate Infusoria," *Journal of Physiology,* 1897, *11:*258–322; and Jennings to Brennemann, 13 Nov. 1896, Jennings Papers (on Haeckel's lectures).

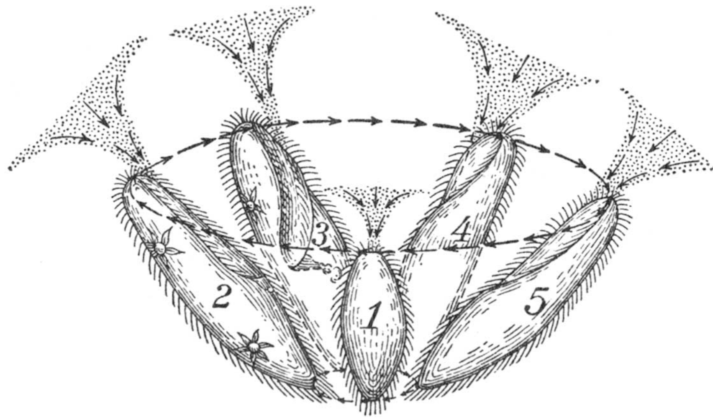

Figure 6. *Motor reaction in a paramecium. From Herbert Spencer Jennings,* Behavior of the Lower Organisms *(1906; Bloomington: Indiana Univ. Press, 1976), p. 50.*

constituted an elaborate series of investigations into the responses of individual protozoa to a wide range of physiological and chemical variables—for example, the variable sensitivity of paramecia to chemicals in relation to the nature of their own culture fluid and the relative strength or weakness of the acidic and alkaline solutions employed. In addition, Jennings paid considerable attention to the anatomical basis of the physiological phenomena he investigated, such as the diverse behaviors of oral and locomotor cilia under the same and different stimuli and the differential sensitivity of different parts of the organism. As the series continued, he used the detailed findings from his first studies of *Paramecium* as a reference point for numerous comparative studies with other protozoa.[52]

In 1899 Jennings offered his initial conclusions on the relative simplicity or complexity of the psychological capacities of protozoa. His response was prompted in part by his reading of the 1889 translation of Binet's *Psychic Life of Micro-organisms* and also by his growing knowledge of investigations such as those by the French scholar Félix Le Dantec, who, like Loeb, viewed the actions of protozoa as nothing more than physicochemical reactions. His own position, which fell between these two interpretations, began to crystallize in the second paper of the series. In a sequence of experiments he demonstrated that the motor reaction in *Paramecium*—consisting always of a backward motion followed by a turn and a subsequent forward motion (see Figure 6)—was not caused by a localization of stimulus, as is found in higher animals: paramecia turn neither toward beneficial stimuli nor away from harmful stimuli. Rather, repeated experimentation demonstrated that the motor reaction, later renamed the "avoiding reaction," was a mechanism internal to the organism, since it could not be varied by any external stimuli. The apparent complexity of the mechanism suggested to him that the primary interest of such investigations was more psychological than physiological. The fixed nature of the motor reaction, however, which he compared to the reactions of an isolated muscle of a frog, indicated that

[52] See, e.g., Jennings, "Studies on Reactions to Stimuli in Unicellular Organisms, I"; Herbert S. Jennings, "Studies on Reactions to Stimuli in Unicellular Organisms, II: The Mechanism of the Motor Reactions of Paramecium," *Amer. J. Physiol.,* 1899, *2:*311–341; and Jennings, "Studies on Reactions to Stimuli in Unicellular Organisms, III: Reactions to Localized Stimuli in Spirostomum and Stentor," *American Naturalist,* 1899, *33:* 373–389.

the reactive behavior of the organism was caused by neither knowledge nor choice. Jennings thus concluded that although *Paramecium* was a psychological being, it was an extremely simple one.[53]

During the next several years Jennings modified his interpretations significantly to emphasize that unicellular organisms react to stimuli as individuals. The transformation in his views occurred as he engaged in extensive new experimental studies and adopted the principles of evolutionary psychology advocated by C. Lloyd Morgan, William James, James Mark Baldwin, and others as his interpretive structure. Jennings first proposed his new interpretation in a collection of essays published in 1904. In the final paper of this group he argued that, when considered in relation to environmental conditions, the avoiding reaction in lower organisms corresponded to the method of "trial and error" viewed by Morgan as central to the development of intelligence in higher animals. According to Morgan and others, he explained, animals employ the method of trial and error until they happen upon a successful means of acting in a specific case. When presented with the same situation at a later time, the animal uses that method without further trials. Jennings insisted, however, that such actions were not limited to cats, dogs, and other higher organisms: "Behavior having the essential features of the method of 'trial and error' is widespread among the lower and lowest organisms, although it does not pass in them so immediately to intelligent action." He reanalyzed several actions of *Paramecium* in terms of the method of trial and error to demonstrate its capacity to explain the behavior, as well as to illustrate the possibility that the mechanisms for "trial" and "error" events were rooted in "physiological states" common across the evolutionary spectrum.[54]

Jennings expanded on his new evolutionary interpretation in his comprehensive book *Behavior of the Lower Organisms,* published in 1906. In this text he brought together the results of his previous studies and those conducted by others in an expanded discussion dedicated largely to psychological questions. In contrast to Verworn's *Protistenstudien,* Jennings's book provided the reader with illustrated accounts of experiments focused on individuals rather than on groups of microorganisms. Typically, these representations were historical: they depicted a series of events, unfolding over time, in which the individual organism exhibited a certain adaptive behavior—for example, the movement of a paramecium to successive positions as it continued to make trials of the environment. Nor did Jennings incorporate Verworn's vivisection technique into his experimental practice. On the contrary, his work aimed to document the individual behavior of the whole organism (see Figure 7).[55]

Although Jennings's treatment of behavior was one source of inspiration for the behaviorist movement that emerged in American psychology a few years later, his conception of behavior differed significantly from many of the views that came to characterize behaviorism. While holding firmly to an objectivist position in both his language and his experimental practice, he maintained that the need to discuss the behavior of lower organisms in objective terms alone had "one possible disadvantage": it resulted in the unfortunate appearance of "an absolute gulf between the behavior of the lower organisms on the one

[53] Jennings, "Studies on Reactions to Stimuli in Unicellular Organisms, III," pp. 388–389; and Jennings, "Studies on Reactions to Stimuli in Unicellular Organisms, II," pp. 338–339. See also Félix Le Dantec, *La matière vivante* (Paris: Masson, 1895).

[54] Herbert S. Jennings, *Contributions to the Study of the Behavior of Lower Organisms,* Publication no. 16 (Washington, D.C.: Carnegie Institution, 1904), pp. 237 (quotation), 238–252. On evolutionary psychology and its proponents see Richards, *Darwin and the Emergence of Evolutionary Theories* (cit. n. 3).

[55] Jennings, *Behavior of the Lower Organisms* (cit. n. 7), pp. 44–51; see also, e.g., pp. 12–19.

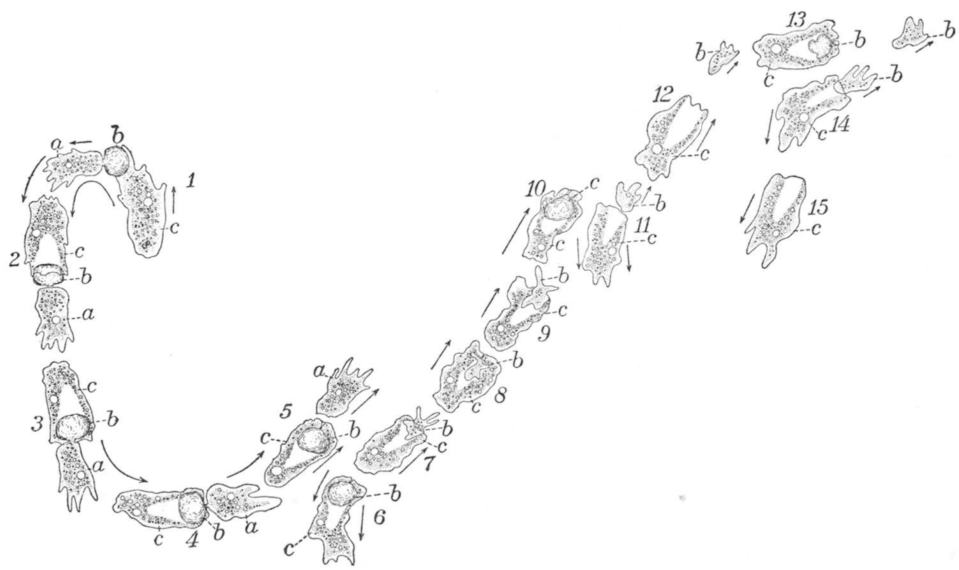

Figure 7. *Representation over time of the pursuit of an amoeba by another for food. From Herbert Spencer Jennings,* Behavior of the Lower Organisms *(1906; Bloomington: Indiana Univ. Press, 1976), p. 16.*

hand, and that of man and higher animals on the other. From a discussion of the behavior of the lower organism in objective terms, compared with a discussion of the behavior of man in subjective terms," he continued, "we get the impression of complete discontinuity between the two." In order to determine whether such a gap was real or an artifact of the use of objective language, he compared features of behavior in the two groups. On the basis of objective features that corresponded with such categories as perception, choice, and attention, he concluded that protozoa did in fact exhibit these behaviors and that there was a clear continuum in the regulatory character of behavior "from the lowest organisms up to man."[56]

Jennings ventured one step further, however, to the question of whether consciousness accompanied these objective phenomena. While acknowledging that there was indeed no way to demonstrate objectively the existence or nonexistence of consciousness in lower organisms, he set out to explore a related question that could be answered: Were the behaviors of lower organisms what we might expect them to be if they did have limited states of consciousness? The answer for Jennings was yes; through our own consciousness, he insisted, it was possible to appreciate the possible nature of the actions of other organisms. In the case of *Paramecium,* for example, the avoiding reaction "makes such an impression that one involuntarily recognizes it as a little subject acting in ways analogous to our own." Speaking from personal experience, he added: "in conducting objective investigations we train ourselves to suppress this impression, but thorough investigation

[56] *Ibid.,* pp. 329, 335. Jennings's evolutionary standpoint led him to reject the possibility of controlling or predicting behavior. On the emergence of behaviorism and Jennings's role in these developments see Donald D. Jensen, "Foreword to the 1962 Edition," in Jennings, *Behavior of the Lower Organisms* (cit. n. 7), pp. xiii–xx. See also John M. O'Donnell, *The Origins of Behaviorism: American Psychology, 1870–1920* (New York: New York Univ. Press, 1985); and Nadine M. Weidman, *Constructing Scientific Psychology: Karl Lashley's Mind–Brain Debates* (Cambridge: Cambridge Univ. Press, 1999), pp. 18–47.

tends to restore it stronger than at first." In making such an argument, Jennings sought to overcome what he believed were the shortcomings of both the nascent behaviorist movement and his own earlier investigations. By drawing on the insights of a developmental evolutionary viewpoint and bringing the observer back into behavioral study, he aimed to close the gap between observer and observed—and thus to surpass the objectivity standards of behavioral research.[57]

THE IMPACT OF PROTOZOAN RESEARCH

During the early twentieth century, Haeckel's program for a cell psychology was exported into a variety of scholarly domains. Verworn, Binet, and Jennings each pursued their respective careers in different contexts, where they further developed the principles acquired in the course of their psychophysiological research on protozoa. In the years following the publication of his studies of protozoa, Verworn continued to confine his investigations to the realm of general physiology. He gradually abandoned work with protozoa, however, turning instead to the publication of several articles on the allegedly cellular-physiological basis of complex psychological functions in humans, such as memory and abstraction.[58] Although Verworn's "molecular psychology" adhered most faithfully to the framework of a cell psychology envisioned by Haeckel, it received no visible support from further experimental studies during his lifetime. It was only in the 1930s that his interest in the biochemical foundation of complex psychological phenomena was taken up and extended by other investigators, in the context of research on the transmission of nerve signals in the brain tissue.[59]

In the late 1890s Binet extended the principles that emerged in his studies of protozoa to the development and promotion of "individual psychology," in which the thematic focus was on the human individual as an organic being that interacts continuously with its environment.[60] Binet assumed that the individual must be understood with respect to this

[57] Jennings, *Behavior of the Lower Organisms,* p. 336. Jennings echoed William James when making these arguments: see *ibid.,* pp. 277–282. On James's views of mind and consciousness as scientific objects in psychology see Eugene Taylor, *William James on Consciousness beyond the Margin* (Princeton; N.J.: Princeton Univ. Press, 1996).

[58] See Max Verworn, "Die cellularphysiologische Grundlage des Gedächtnisses," *Zeitschrift für Allgemeine Physiologie,* 1907, *6:*119–139; and Verworn, "Die zellularphysiologischen Grundlagen des Abstraktionsprozesses," *ibid.,* 1913, *14:*277–296. More broadly, see Verworn, *Die Mechanik des Geisteslebens* (Leipzig: Teubner, 1907). Other aspects of Verworn's later work, however, remained closely tied to the historical dimension of Haeckel's *Entwicklungslehre;* he published several studies on archaeology and the natural history of art in which he revealed his interest in the history of the human mind. See, e.g., Verworn, *Die Anfänge der Kunst: Ein Vortrag* (Jena: Fischer, 1909); and Verworn, *Zur Psychologie der primitiven Kunst* (Jena: Fischer, 1917).

[59] On the relation of research on protozoa to the brain sciences see Sandra Black, "Pseudopodes and Synapses: The Amoeboid Theories of Neuronal Mobility and the Early Formulation of the Synapse Concept, 1894–1900," *Bulletin of the History of Medicine,* 1981, *55:*34–58; Sven Dierig, "Extending the Neuron Doctrine: Carl Ludwig Schleich and His Reflections on Neuroglia at the Inception of the Neural-Network Concept in 1894," *Trends in Neurosciences,* 1994, *17:*449–453; and Cornelius Borck, "Fühlfäden und Fangarme: Metaphern des Organischen als Dispositiv der Hirnforschung," in *Ecce Cortex: Beiträge zur Geschichte des modernen Gehirns,* ed. Michael Hagner (Göttingen: Wallstein, 1999), pp. 144–176. More generally, see Olaf Breidbach, *Die Materialisierung des Ichs: Zur Geschichte der Hirnforschung im 19. und 20. Jahrhundert* (Frankfurt am Main: Suhrkamp, 1997), pp. 195–202.

[60] Alfred Binet and Victor Henri, "La psychologie individuelle," *Rev. Phil. Fr. Étrang.,* 1895, *2:*411–465; Binet, "Psychologie individuelle: La description d'un objet," *ibid.,* 1896/1897, *3:*296–332; and Binet, "La psychologie individuelle," in *Dritter Internationaler Congress für Psychologie in München vom 4. bis 7. August 1896* (Munich: Lehmann, 1897), pp. 244–246. The term "individual psychology" later became closely linked to the psychoanalytical doctrine of Alfred Adler. See Ellenberger, *Discovery of the Unconscious* (cit. n. 45), pp. 571–656.

interaction and that individuality is based largely on organic or physiological characteristics that cannot be reduced to mechanical or chemical processes. He often complemented and sometimes even replaced this biological conception of the individual with a historical viewpoint, according to which organic individuality was defined in terms of the development of the being in question. In his later writings Binet advocated a conception of intelligence as the evolving ability of the individual to cope with its environment. He developed these ideas in his *Étude expérimentale de l'intelligence* [*Experimental Study of Intelligence*], published in 1903, where he showed how intellectual activity is determined by personal "themes" highly characteristic of the development of each individual. He concluded from these studies that there are different types of intelligence, which he assumed were based on organic factors. Binet's contributions laid the foundation for a biologically based science of developmental psychology of which Jean Piaget is perhaps the most prominent heir.[61]

Like Binet, Jennings remained focused on questions of individuality when he turned to a new field of scientific inquiry in 1907. After completing his behavioral studies of microorganisms, Jennings took up genetic investigations of protozoa, which he continued throughout the remainder of his career. Unlike most genetic studies of the period, however, his investigations maintained a focus on the individual organism, especially in relation to its hereditary adaptiveness to environmental change. In the late 1910s Jennings extended the biological conception of individuality arising from his studies of the behavior and genetics of protozoa to the issues of child education and school reform. In an article entitled "The Biology of Children in Relation to Education," he argued that individuality is biologically based and that children accordingly need an educational system that encourages the expression rather than the suppression of that individuality. Such a system, he argued, was best achieved through play, activity, and the maintenance of good environmental conditions (most especially good nutrition, the absence of germs, proper heat, and fresh air), which would enable the child to acquire the ability to adapt to diverse situations as they arose in the course of his or her development.[62]

Jennings continued to advocate these views throughout the 1920s, as he engaged in public critiques of many of the principles underlying the genetic determinism of the eugenics movement in the United States. Speaking and writing for audiences of social workers, child-play advocates, and other proponents of environmental reform, he maintained that education and environment were critical in determining the potential not only of individuals but also of their descendants, since he conceived of heredity as an adaptive and developmental process.[63]

[61] See Alfred Binet, *L'étude expérimentale de l'intelligence* (Paris: Schleicher, 1903), pp. 9–51. In his genetic psychology, Piaget considered knowledge to be a biological function of the whole organism and to be defined by the processes of assimilation and accommodation, which interact with the environment. On Piaget see Fernando Vidal, *Piaget before Piaget* (Cambridge, Mass.: Harvard Univ. Press, 1994). More generally, see also Edna Heidbreder, "Functionalism," in *Schools of Psychology: A Symposium,* ed. David L. Krantz (New York: Meredith, 1969), pp. 35–50; and Robert H. Wozniak, "Introduction," in *Mind, Adaptation, and Childhood,* ed. Wozniak (London: Routledge/Thoemmes, 1995), pp. ix–xxxv.

[62] Herbert S. Jennings, "The Biology of Children in Relation to Education," in Jennings, John B. Watson, Adolf Meyer, and William I. Thomas, *Suggestions of Modern Science Concerning Education* (New York: Macmillan, 1917), pp. 1–50. For the genetic investigations see, e.g., Jennings, "Heredity, Variation, and Evolution in Protozoa, I: The Fate of New Structural Characters in Paramecium, in Connection with the Problem of the Inheritance of Acquired Characters in Unicellular Organisms," *Journal of Experimental Zoology,* 1908, *5:*577–632; and Jennings, "Heredity, Variation, and the Results of Selection in the Uniparental Reproduction of *Difflugia corona,*" *Genetics,* 1916, *1:*407–534.

[63] See, e.g., Herbert S. Jennings, "Heredity and Environment," *Scientific Monthly,* 1924, *19:*226–238; Jennings, *Prometheus; or, Biology and the Advancement of Man* (New York: Dutton, 1925); and Jennings, "Health Progress and Race Progress," *Journal of Heredity,* 1927, *18:*271–276.

In addition to those investigators who engaged directly in psychophysiological research on protozoa, many other scholars drew on studies of unicellular organisms when illustrating their own arguments about psychological principles and processes. Important among these was the German philosopher Friedrich Nietzsche, who referred to "primitive nutrition" in protozoa as the "simplest case" of voluntary movement in his well-known collection of fragmentary writings, *Der Wille zur Macht* [*The Will to Power*], published in 1906. "The protoplasm," Nietzsche explained in writings dating to the late 1880s, "extends its pseudopods in order to seek out something that resists it—not because of hunger, but because of the will to power." In other writings from the same period, he described the physiological basis of perception, thought, and judgment as a process of assimilation similar to "the incorporation of acquired matter into the amoeba."[64]

In the early 1890s the American philosopher Charles Sanders Peirce likewise reflected on the protoplasmic basis of psychological functions. In the article "Man's Glassy Essence," published in the *Monist* in 1892, Peirce aimed to formulate—in a manner similar to Verworn—a "molecular theory of protoplasm" that would account for the relationship between the "psychical and physical aspects" of matter. On the basis of his understanding of the properties of cells and unicellular organisms, he maintained that there was no intrinsic reason why it would not be possible to produce protoplasm artificially in the laboratory. Yet he also argued that this living substance is capable of "extraordinary" properties, such as the formation of habits, feeling, and "all the functions of mind." Like Jennings, Peirce turned to the writings of the evolutionary psychologists William James and James Mark Baldwin to assist him in resolving the tension between these claims. He abandoned his attempt to deduce psychological phenomena from physical events, since he found that a purely mechanistic philosophy could not adequately represent the unstable condition of protoplasm. Instead he argued, in a manner similar to Haeckel and Verworn, that "physical events are but degraded or undeveloped forms of psychical events." Peirce contended that the mind and personality are therefore inseparable from matter. What is required for the existence of a person, he concluded, is that "the feelings out of which [a person] is constructed should be in close enough connection to influence one another," just as feelings spread via reactions among neighboring molecules of protoplasm in cells and protozoa.[65]

The reception of Jennings's behavioral studies was somewhat less speculative. In reintroducing consciousness to animal psychology at a time when behaviorists were trying to expunge it from psychology more generally, Jennings's 1906 book met with sharp criticism. The critics focused on disciplinary and methodological issues and presented them-

[64] Friedrich Nietzsche, *Der Wille zur Macht: Versuch zu einer Umwerthung aller Werte (Aus dem Nachlaß 1884/88),* Vol. 2 (Leipzig: Kröner, 1906), p. 518; and Nietzsche, *Sämtliche Werke: Kritische Studienausgabe,* ed. Giorgio Colli and Mazzino Montinari, 15 vols., Vol. 12: *Nachgelassene Fragmente 1885–1887* (Munich: Deutscher Taschenbuch Verlag, 1980), p. 209. At that time Nietzsche was in close contact with the physiologist Joseph Paneth, a student of Brücke, whom he visited frequently at the marine station at Villefranche-sur-Mer, near Nice. On Paneth and Nietzsche see Richard Frank Krummel, "Joseph Paneth über seine Begegnung mit Nietzsche in der Zarathustra-Zeit," *Nietzsche-Studien,* 1988, *17:*478–495.

[65] Charles Sanders Peirce, "Man's Glassy Essence," in *Collected Papers of Charles Sanders Peirce,* ed. Charles Hartshorne and Paul Weiss, 8 vols., Vol. 6: *Scientific Metaphysics* (Cambridge, Mass.: Harvard Univ. Press, Belknap, 1965), pp. 155–177, on pp. 155, 167, 173, 176. On Peirce's evolutionary cosmology see also Peirce, "The Architecture of Theories," *ibid.,* pp. 11–27; Peirce, "The Doctrine of Necessity Examined," *ibid.,* pp. 28–45; Peirce, "The Law of Mind," *ibid.,* pp. 86–113; and Peirce, "Evolutionary Love," *ibid.,* pp. 190–215. These essays appeared in series with "Man's Glassy Essence" in the *Monist* in 1891–1893. See esp. "Law of Mind," pp. 101–102, for Peirce's discussion of the spatial extension of feeling in terms of the feelings of amoebas and other protoplasmic beings.

selves as falling into two camps: those who upheld some form of tropism, a position championed most aggressively by Jacques Loeb; and those who were proponents of the rising behaviorism. Both sides criticized the psychological dimension of Jennings's studies, albeit with different arguments. Whereas Loeb and his supporters argued principally against the use of psychological concepts in a domain they thought was purely physiological or even chemical, behaviorists opposed Jennings's attempt to incorporate phenomena that, in their eyes, were not "objective manifestations" of consciousness; in both cases, Jennings's critics ignored or rejected his evolutionary epistemology.[66]

Outside of these two camps, however, scholars responded positively to Jennings's studies. In particular, theoretical works that argued against reductionism in the life sciences repeatedly cited his studies in support of a biology or psychology more focused on the relative autonomy and dynamic functions of living beings. Thus in his *Évolution créatrice* [*Creative Evolution*], published in 1907, the renowned French philosopher Henri Bergson cited Jennings's studies of protozoa when arguing against the assumption that the behavior of living beings can be explained by physical and chemical processes. Similarly, the German phenomenologist Max Scheler quoted Jennings in his 1928 book *Die Stellung des Menschen im Kosmos* [*The Position of Man in the Universe*] when explaining that instincts are "amechanical," that they cannot be reduced to a combination of single reflexes—"chain reflexes" (*Kettenreflexe*)—or to mechanical tropisms. And in 1934 Kurt Goldstein drew on Jennings's investigations to emphasize the holistic nature of organisms' reactions to their surroundings in his *Die Struktur des Organismus* [*The Structure of the Organism*].[67]

Perhaps the most striking example of the traces left on psychological discourse by studies of protozoa is the case of psychoanalysis. Beginning with his early anatomical and physiological studies on several lower metazoa, Sigmund Freud incorporated biological and evolutionary reasoning into his conceptual framework. A former student of Brücke, Freud not only advocated an evolutionary conception of the development of organisms and their various nervous functions but was convinced of the general validity of Haeckel's biogenetic law. He continued to draw on these resources in the course of his career, and a Haeckelian conception of the organic individual played an important role in his later theories.[68]

[66] On the reception of Jennings's book see Jensen, "Foreword to the 1962 Edition" (cit. n. 56), pp. x–xiv. Tropism theories aimed to generalize the physicochemical phenomena that determine the specific orientation taken by an organism in relation to external sources of stimulation, such as light or gravity. For contemporary views see, e.g., Harry Beal Torry, "The Method of Trial and the Tropism Hypothesis," *Science,* 1907, *26:*313–323; George H. Parker, review of Jennings, *Behavior of the Lower Organisms, ibid.,* p. 548; J. B. Watson, review of Jennings, *Behavior of the Lower Organisms, Psychological Bulletin,* 1907, *4:*288–291; Georges Bohn, *La naissance de l'intelligence* (Paris: Flammarion, 1909); and Jacques Loeb, "Die Bedeutung der Tropismen für die Psychologie," in *Compte rendus du VIème Congrès international de psychologie* (Geneva: Kündig, 1909), pp. 281–306, rpt. as "The Significance of Tropisms for Psychology," in Loeb, *Mechanistic Conception of Life,* ed. Fleming (cit. n. 28), pp. 35–62.

[67] Henri Bergson, *L'évolution créatrice,* in *Oeuvres: Édition du centenaire* (Paris: Presses Univ. France, 1959), pp. 487–809, esp. pp. 516–532; Max Scheler, "Die Stellung des Menschen im Kosmos," in *Gesammelte Werke,* ed. Manfred S. Frings, Vol. 9: *Späte Schriften* (Bern/Munich: Francke, 1976), pp. 7–71, esp. pp. 18–20; and Kurt Goldstein, *Der Aufbau des Organismus: Einführung in die Biologie unter besonderer Berücksichtigung der Erfahrungen am kranken Menschen* (The Hague: Nijhoff, 1934), p. 137. Scheler was personally acquainted with Frederik Buytendijk, a Dutch physiologist who also was engaged in psychological research on protozoa. On Buytendijk and Scheler see Wilhelm J. M. Dekkers, *Het bezielde lichaam: Het ontwerp van een antropologische fysiologie en geneeskunde volgens F. J. J. Buytendijk* (Zeist: Kerckebosch, 1985), pp. 130–135; more broadly, see G. Thinès and R. Zayan, "Frederik J. J. Buytendijk's Contribution to Animal Behavior: Animal Psychology or Ethology?" *Acta Biotheoretica,* 1975, *24:*86–99. On Goldstein and the context of his work see Anne Harrington, *Reenchanted Science: Holism in German Culture from Wilhelm II to Hitler* (Princeton, N.J.: Princeton Univ. Press, 1996), esp. pp. 140–174.

[68] On Freud's reception of Darwinism and Haeckelism see Frank J. Sulloway, *Freud: Biologist of the Mind*

Freud undoubtedly was inspired not only by Brücke and Haeckel but also by the psychophysiological studies of his contemporaries, such as Jennings. In September 1909 he made his only trip to the United States to participate in the celebration of the twentieth anniversary of the founding of Clark University, organized by G. Stanley Hall. Jennings was also invited to the event, where both he and Freud were awarded honorary degrees for their contributions to psychology. In the course of the celebration Freud presented a series of five short lectures on psychoanalysis that gave a general overview of his doctrine. In his contribution Jennings lectured on the diverse "ideals" underlying the different conclusions he and Loeb and his followers had reached regarding the behavior of lower organisms, stressing the importance of a focus on the organic individual for the sound biological foundation of psychology.[69]

The insights that Freud gleaned from psychophysiological research on protozoa during this period appear to have been quite far reaching. Beginning in the mid 1910s, he employed microorganisms as models for explaining the structure and function of the psyche and its interaction with the environment. When he transformed his early conception of the three systems of the "unconscious, pre-conscious, conscious" laid out in the *Traumdeutung* [*The Interpretation of Dreams*] in 1900 into the model of the three instances of the "Id, Ego, Super-Ego" introduced in *Das Ich und das Es* [*The Ego and the Id*] in 1923, he repeatedly described the ego as a protozoan. In his 1914 text "Zur Einführung des Narzißmus" ["On Narcissism: An Introduction"], for example, he illustrated his theory of primary narcissism by pointing to the example of "protoplasmic animalcules" (*Protoplasmatierchen*). According to Freud, there is an original libidinal "cathexis"—an emotional investment—in the ego that relates to investments in "objects" (primarily other people) in the same way that "the body of an amoeba is related to the pseudopodia which it puts out." Insofar as there is an original libido investment, he argued, it always remains with the ego; in other words, although the ego reaches out for objects, it nevertheless also always pulls back from them and remains autonomous.[70]

Freud drew a similar comparison in 1918 in his *Vorlesungen zur Einführung in die Psychoanalyse* [*Introductory Lectures on Psychoanalysis*]. In order to illustrate the relation between the "ego-libido" and the "object-libido," he put forth what he called an "analogy from zoology":

> Think of those simplest of living organisms [the amoebas] which consist of a little-differentiated globule of protoplasmic substance. They put out protrusions, known as pseudopodia, into which they cause the substance of their body to flow over. They are able, however, to withdraw the

(New York: Basic, 1979); and Lucille Ritvo, *Darwin's Influence on Freud: A Tale of Two Sciences* (New Haven, Conn.: Yale Univ. Press, 1990). On Freud's relation to evolutionism and physiology see S. P. Fullinwinder, "Darwin Faces Kant: A Study in Nineteenth-Century Physiology," *British Journal for the History of Science,* 1991, *24:*21–44; and Joachim Widder, "Die Erhaltung der Erregungssumme: Die Physiologen Ernst W. Brücke, Sigmund Exner und Ernst Fleichl von Marxow als Lehrer Sigmund Freuds," *Sudhoffs Archiv: Zeitschrift für Wissenschaftsgeschichte,* 1999, *83:*152–170.

[69] Sigmund Freud, "The Origin and Development of Psychoanalysis," *Amer. J. Psychol.,* 1910, *21:*181–218; and Herbert S. Jennings, "Diverse Ideals in the Study of Behavior in Lower Organisms," *ibid.,* pp. 349–370. On the Clark University anniversary celebration see Dorothy Ross, *G. Stanley Hall: The Psychologist as Prophet* (Chicago: Univ. Chicago Press, 1972), esp. pp. 386–394.

[70] Sigmund Freud, *The Interpretation of Dreams,* in *The Standard Edition of the Complete Psychological Works,* ed. and trans. James Strachey *et al.,* 24 vols. (London: Hogarth Press and the Institute of Psycho-Analysis, 1953–1974), Vol. 5, esp. pp. 509–621; Freud, "The Ego and the Id," *ibid.,* Vol. 19, pp. 1–66; Freud, "On Narcissism: An Introduction," *ibid.,* Vol. 14, pp. 67–102, on p. 75; Ellenberger, *Discovery of the Unconscious* (cit. n. 45), pp. 510–518; and Ernest Jones, *Sigmund Freud: Life and Works,* 3 vols. (London: Hogarth Press, 1954–57), Vol. 3, pp. 286–308.

> protrusions once more and form themselves again into a globule. We compare the putting-out of these protrusions, then, to the emission of libido onto objects while the main mass of libido can remain in the ego; and we suppose that in normal circumstances ego-libido can be transformed unhindered into object-libido and that this can once more be taken back into the ego.

In this comparison, protozoan behavior and the first stages of the developing human individual are compared. On the basis of this parallel, Freud assumed that there was a primary emotional self-relatedness and autonomy in human beings that was not subject to exchange with the surrounding world: the object-libido is only extended ego-libido, and contact between the individual and its milieu does not compromise the essential autonomy of the individual.[71]

CONCLUSION

The repeated and often puzzling appearance of protozoa in the psychological and philosophical writings of scholars such as Freud, Nietzsche, and Peirce about such problems as the nature of the ego, the will, and the personality can be traced to the extensive history of protozoa as objects that straddled fundamental boundaries in the natural world. Conceived since the eighteenth century as both individual entities and elemental parts and, later, as both cells and individual organisms, protozoa became intimately associated with conceptions of organic individuality and were viewed as ideal units for the study of elementary physiological functions.

Following the advent of evolutionism in the last decades of the nineteenth century, these associations receded into the background as the belief that protozoa exemplified the simplest forms of psychological life moved into the foreground. Situated during that period on the border between physiology and psychology, unicellular organisms provoked not only experimental studies of the physiological basis of psychological individuality but also investigations of specific psychological functions such as choice, thought, and feeling. Although the scientific and philosophical developments that made these studies possible—including the rise of general physiology, evolutionism, and monism—converged for less than fifty years on protozoa as research objects, the concepts and methods exported from psychophysiological studies of protozoa played an important role in psychological and philosophical scholarship throughout the twentieth century.

From Peirce's theory of the nature of personality to Binet's leading role in the establishment of the fields of individual and developmental psychology, and from Jennings's developmentalist contribution to child-welfare reform to Freud's model of the structure and function of the psychological apparatus, protozoa provoked novel associations and provided conceptual resources for major developments in twentieth-century psychological, philosophical, and even social and political thought. By examining the history of physiological psychology from the perspective of research organisms, we see that the connections between physiology, psychology, and philosophy in the late nineteenth century generated a wealth of ideas and practices far beyond those that the well-known case of Wundt suggests.

[71] Sigmund Freud, *Introductory Lectures on Psycho-Analysis* (Pt. 3), in *Standard Edition,* ed. and trans. Strachey *et al.,* Vol. 16, p. 416 (the bracketed material was added by the editors of the *Standard Edition*). Freud further developed aspects of his comparison between the "ego" and the "protoplasma animalcule" in later texts. In "Jenseits des Lustprinzips" ["Beyond the Pleasure Principle"], for example, he alluded to the Haeckelian notion of "sensitive strings" (see note 25, above) when drawing a parallel between the sense organs in higher organisms and the "feelers," or pseudopods, of protozoa. He also compared the ego-function of choice and judgment to the nutrition-seeking behavior of protozoa. See Freud, "Beyond the Pleasure Principle," in *Standard Edition,* ed. and trans. Strachey *et al.,* Vol. 18, pp. 1–64, esp. pp. 24–29; Freud, "A Note upon the Mystic Writing Pad," *ibid.,* Vol. 19, pp. 227–232, esp. p. 231; and Freud, "Negation," *ibid.,* pp. 233–239, esp. pp. 237–238.